

THE SIRENIAN FEEDING APPARATUS: FUNCTIONAL MORPHOLOGY OF FEEDING  
INVOLVING PERIORAL BRISTLES AND ASSOCIATED STRUCTURES

By

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## DEDICATION

I dedicate this work to the memory of J. Rooker (known to us simply as "Rooker") and to sirenian conservation. Rooker was a subject involved in the study during the 1993 sampling year at Lowry Park Zoological Gardens. Rooker died during the red tide event in May of 1996; approximately 140 other manatees also died. During his rehabilitation at Lowry Park Zoo, Rooker provided much information regarding the mechanism of manatee feeding and use of the perioral bristles. The "mortality incident" involving the red tide event in southwest Florida during the summer of 1996 should serve as a reminder that the Florida manatee population and the status of all sirenians is precarious. Although some estimates suggest that the Florida manatee population may be stable, annual mortality numbers as well as habitat degradation continue to increase. Sirenian conservation and research efforts must continue.

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Major Department: Physiological Sciences

The anatomy of the feeding apparatus and behavioral components of perioral bristle used during feeding in Florida manatees and other sirenians was examined. Bristles, bristle-like hairs and body hairs were characterized. Bristle fields are located in six discrete locations in the perioral region. Branches of the infraorbital nerve and the mental branches of the inferior alveolar nerve terminate at the bases of the bristles on the upper bristle pad and the lower bristle pad, respectively. The dorsal and ventral buccal branches of the facial nerve innervate the associated musculature. Behavioral use of perioral bristles was analyzed by observing captive manatees feeding upon aquatic vegetation normally eaten in the wild and manipulating inanimate objects. Feeding involved the large and robust perioral bristle fields of the upper lip moving in a prehensile manner. Bristle use by manatees feeding on submerged vegetation differed from that seen during feeding on floating vegetation. The duration of bristle use showed variation depending upon the



vegetation consumed. Mean feeding cycle length for all manatees feeding on all species of submerged vegetation was 610 ms ( $\pm$ S.D. 52.9). Body length effected the mean feeding cycle length. Facial musculature was examined in order to develop a functional model of perioral bristle use. A new muscle, *M. centralis nasi*, has been named and is an integral part of perioral bristle movement. The prehensile ability of Florida manatees can be explained in the context of a muscular hydrostat. Feeding was examined in dugongs which also involved perioral bristle fields of the upper lip in a prehensile manner. Pattern of bristle use differed from that of the manatee. The mean dugong feeding cycle length (791 ms) was statistically different compared to manatees (610 ms). Feeding behavior in Amazonian and Antillean manatees was consistent with that from Florida manatees. Florida manatees, dugongs, walruses and bearded seals speculated to share a suite of convergent ecomorphological characteristics. Such comparisons can be used to speculate upon the function of vibrissae in all mammals. A spectrum of motor and sensory components of vibrissal use in all mammals based on natural history traits is also proposed.

## CHAPTER 1 INTRODUCTION AND BACKGROUND

### Introduction

Among mammals, aquatic herbivory is a unique niche compared to terrestrial herbivory; sirenians (manatees and dugongs) are the only extant marine mammal herbivores in existence. The aquatic habitat places different selection pressures on form and function. It is obvious that certain convergent patterns are required of all marine mammals; all are sleek and fusiform in shape. However, most marine mammals are carnivores. To be a successful marine mammal aquatic herbivore requires a variety of adaptations and solutions to browse and graze upon underwater meadows efficiently. Research on sirenians has been limited compared to that on some other marine mammal taxa. Sirenians have been called the forgotten group of marine mammals (Reynolds and Odell, 1991). Only recently has interest in these unique marine mammals become widespread. Our limited knowledge of sirenian natural history is exemplified by the fact that, although sirenians spend a large portion of their day feeding, currently we do not completely understand the mechanisms which allow a mammal to consume vegetation underwater. The mechanics of gathering and processing food directly affect the fitness of the organism (Wainwright, 1994). How do sirenians efficiently harvest vegetation and what are the anatomical and behavioral components involved? This research focuses on these questions.

## Integrative Relationships Among Morphology, Behavior and Ecology

Understanding structure and function of organisms is one of the oldest and still active areas of biology (Wainwright and Reilly, 1994). Morphology can constrain or increase an organism's behavioral capacity to utilize its resources (Wainwright and Reilly, 1994). Functional morphology is ". . . the study of form, structure and function and their relationships to one another (Wainwright, 1988)." The relationships among morphology, behavior and ecology can be complex. Once the relationship between morphology and behavior is understood, behavioral performance can be related to the ecology of the organism in two ways. First, behavioral limitations may constrain the types of habitats that can be exploited. Second, they may effect the fitness of the organism with "varying degrees of directness" by influencing the amount of energy available for reproductive output (Wainwright, 1994).

Geoffroy Saint-Hilaire coined the term "Ethology" in 1854 to describe the interrelationships of structure, behavior and mode of life form (often called the biological trinity), which form an integrative adaptive unity (Ewer, 1968). Saint-Hilaire's emphasis on structure and his definition of ethology was, in effect, structural adaptation. "Modern" ethology focused more on the biological study of behavior itself (Tinbergen, 1963) and integrated the concept of evolution into the biological trinity; structure and "mode of life form" became less of a consideration (Ewer, 1968). There are many definitions of ethology. Gould (1982) defined ethology as the study of the mechanisms and evolution of behavior. Alcock (1989) defined ethology as the study of the proximal mechanisms and adaptive value of animal behavior and Allaby (1994) phrased it as "the scientific study of the behavior of animals in their normal environment, including all the processes, internal and external, by which they

respond to changes in their environment." Wilson (1980) predicted that the older synthesis of ethology, which integrated neurobiology and behavioral ecology, would split into two separate disciplines, a mechanistic group (neurobiology) and an evolutionary group (behavioral ecology).

The definition of ecology has been blurred since the origin of the field. Ernst Haeckel first defined Ecology in 1869 based on the word *Oikos*, which means home (Haeckel, 1870):

By ecology we mean the body of knowledge concerning the economy of nature - the investigation of the total relations of the animal both to inorganic and its organic environment; including, above all, its friendly and inimical relations with those animals and plants with which it comes directly or indirectly into contact - in a word, ecology is the study of all those complex interrelationships referred to by Darwin as the conditions of the struggle for existence.

Popular definitions of ecology are also numerous. Webster (1966) defined ecology as "the totality of patterns or relations between organisms and their environment." Allaby (1994) defined ecology as "the interrelationships among organisms and between organisms, and between them and all aspects, living and non-living, of their environment." The key words in all of these definitions are "relationships" and "interactions." In the context of this dissertation, ecology will refer to the relationships between sirenian foraging behavior and their environment.

Behavioral ecology can be viewed as that part of ethology that addresses the evolution and adaptive value of behavior. It is ". . . the pursuit of the design principles by which evolution has fashioned the special combination of habitat choice, diet and foraging strategy, social organization and reproductive strategy, mating system and parental investment, which makes each species different (Gould, 1982)." Alcock (1989) defined behavioral ecology as "the study of the adaptive value of behavioral attributes in solving environmental

obstacles to reproduction by individuals." and Allaby (1994) described it as "the study of the behaviour of an organism in its natural habitat and the application of behavioural theories (e.g., game theory) to particular activities (e.g., foraging)."

Recently, a new field, ecological morphology (also called ecomorphology), has emerged as a synthesis of organismal functional morphology, physiology and biomechanics. This has been due to an increasing need in these fields to (1) make observations and interpretations concerning how organisms function within an environmentally and historically relevant context and (2) understand the ecological and evolutionary consequences of organismal form (Figure 1) (Wainwright and Reilly, 1994).

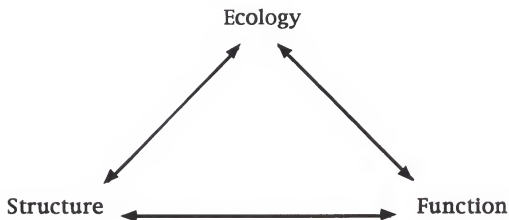


Figure 1. Integrative relationships of ecomorphology.

Ricklefs and Miles (1994) considered ecomorphology from an ecologist's perspective, and stated that there are three goals of ecomorphological analyses: (1) estimation of ecological relationships among species from their positions in morphological space, that is, to make ecological inferences from morphological pattern, (2) measurement of the ecology-morphology correlation as a means of

validating the first goal, and (3) elucidation of the functional relationship between morphology and ecology as it is mediated by the behavior and performance (ethotype) of the organism (Ricklefs and Miles, 1994).

Ecomorphology is simply a new term for the older acknowledgment of a need for a holistic view that integrates separate disciplines of biology. The objective of this dissertation is to integrate several of these fields of study (morphology, behavior, and ecology) to systematically examine the structure and function of the sirenian feeding apparatus to gain new insight into sirenian foraging ecology.

### Background

#### Order Sirenia--Taxonomy

The Order Sirenia (manatees and dugongs) represents the only living taxon of obligate marine mammal herbivores. It is a member of the Superorder Paenungulata (Simpson, 1945) or the Superorder Subungulata (Romer, 1966) and, among extant taxa, is most closely related to elephants and hyraxes. The order is comprised of two families, Trichechidae (manatees) and Dugongidae (dugongs). Three species of manatees are extant- the West Indian manatee (*Trichechus manatus*), the Amazonian manatee (*T. inunguis*) and the West African manatee (*T. senegalensis*). The West Indian manatee (*Trichechus manatus*) is comprised of two subspecies, the Florida manatee (*T. manatus latirostris*) and the Antillean manatee (*T. m. manatus*). The Family Dugongidae is represented by a single extant species, the dugong (*Dugong dugon*) and the recently extinct Steller's sea cow (*Hydrodamalis gigas*).

## Distribution

The Florida manatee is the best studied sirenian (O'Shea *et al.*, 1995). Florida lies at the northern limit of the range of the West Indian manatee during the winter months. The year-round range of Florida manatees is restricted to the peninsula of Florida and southern Georgia. During the summer, the Florida manatee may range as far north as Rhode Island and as far west as Louisiana (Lefebvre *et al.*, 1989; Jim Reid, personal communication).

The Antillean manatee is found along the Caribbean coastline and rivers of Central America, the northern coast of South America, and the greater Caribbean area. Specifically, Antillean manatees can be found from the Texas-Mexico border south to Espiritu Santo, Brazil as well as around the islands of Cuba, Haiti, Dominican Republic, Jamaica, and Puerto Rico. There is some evidence that manatees may occasionally visit the Virgin Islands and the Bahamas, but little data exist to support such contentions. Antillean manatees are unevenly distributed along the Lesser Antilles (e.g., Trinidad and Tobago) but the numbers of these populations are not well known (Lefebvre *et al.*, 1989).

The distribution of the Amazonian manatee is confined to the freshwater tributaries of Brazil, Colombia, Peru and Ecuador, specifically the following river systems: Tocantins, Xingu, Papajo, Nhamunda, Madeira, Negro, Branco, Takatu, Amazon, Putumayo, and Caqueta rivers, the lower Apaporis, Napo, Tigre, Maranon, Samiria, Pacaya Ucayali, and Huallago rivers, and the lagoons near the Rio Aguarico and Rio Cuyabeno rivers (Reynolds and Odell, 1991). It is the only sirenian species to live solely in a freshwater habitat. Amazonian manatees prefer the flood-plain lakes and channels of the white-water river systems. The name "white-water" is given to regions where the water quality is

characterized by fine suspended inorganic solids which color the water white (Prance and Lovejoy, 1985).

The West African manatee is distributed along the coast and rivers of African's west coast from Senegal to Angola. Its distribution is wide and covers both freshwater and marine systems in over twenty countries (Reynolds and Odell, 1991). Populations of West African manatees seem variable and discontinuous, perhaps due to variability of habitat and human related disturbances and hunting (Reynolds and Odell, 1991).

The dugong (*Dugong dugon*) is widely but unevenly distributed along the western Pacific and Indian oceans. Its range covers over 43 countries (Nishiwaki *et al.*, 1979; Nishiwaki and Marsh, 1985). The largest population is along the northern coast of Australia, from Moreton Bay on the east coast to Shark Bay on the western coast. Dugongs range throughout Indonesia, Micronesia and Melanesia to the Persian Gulf and Red Sea, and along the eastern coast of Africa south to Mozambique (Nishiwaki *et al.*, 1979; Nishiwaki and Marsh, 1985).

Steller's Sea Cow (*Hydrodamalis gigas*) was the only Recent sirenian to inhabit non-tropical waters. It was once found throughout the Aleutian islands of the Gulf of Alaska. Its distribution was likely tied to the distribution of marine kelp (Anderson, 1995). The population and distribution of Steller's Sea Cow was likely much reduced when they were discovered and hunted to extinction by Russian sailors seeking otter and seal pelts during the mid-1700's (Steller, 1899, 1925).



## Natural History

Since the Florida manatee has been the most studied sirenian (O'Shea *et al.*, 1995), much of this section regarding manatees will be based on data from Florida manatees. All sirenians are large, k-selected herbivorous marine mammals and are long lived. Wild manatees can live over fifty years (Marmontel *et al.*, 1996). The oldest living captive Florida manatee is over 45 years old (Reynolds and Odell, 1991). Dugongs are estimated to live sixty to seventy years (Marsh, 1980).

West Indian and African manatees inhabit both coastal marine and riverine habitats and feed upon floating and submerged vegetation in both systems (Best, 1981). Amazonian manatees feed primarily upon floating vegetation. Evidence suggests that Amazonian manatees may fast for several months during the dry season due to limited availability of plants (Best, 1983). The dugong is the only sirenian to inhabit a solely marine environment (Marsh *et al.*, 1977). Dugongs are seagrass specialists and possess an unusual facial anatomy that includes a ventrally deflected rostrum for bottom feeding (Domning, 1976; Marsh *et al.*, 1977).

Manatees and dugongs have a slow rate of reproduction. Florida male manatees reach sexual maturity as early as three to five years and females may reach sexually mature between three and four years (Hartman, 1979; Hernandez *et al.*, 1995; Marmontel, 1995; Rathbun *et al.*, 1995). Mating can occur throughout the year, although more calves are observed in the spring and summer (Hartman, 1979; Rathbun *et al.*, 1995). Seasonality of mating and calving does occur in dugongs; males appear more spermatogenically active from June to January and calves are usually born August through November (Marsh, 1995). The incidence of breeding in Amazonian manatees is affected by

the extreme wet-dry seasons of the tropics. Calves are usually born between the months of December and July, as water levels rise (Best, 1982). Gestation of all sirenians is approximately eleven to thirteen months and the sex ratio is usually 1:1 (Hartman, 1979; Marmontel *et al.*, 1992; Marsh, 1995; Rathbun *et al.*, 1995). Calves are usually suckled up to a year but may begin to feed much earlier (Hartman, 1979). Calves may stay with their mothers for up to two years, and the calving interval ranges from two to five years (Rathbun *et al.*, 1995). In contrast, dugongs do not become sexually mature until nine to ten years of age (males and females) and the calving interval ranges from three to seven years (Marsh, 1995).

#### General Morphology of the Sirenian Feeding Apparatus

The dugong's rostrum is turned-down by  $70^{\circ}$  relative to the horizontal axis of the body (Domning, 1976) and ends in a broad flattened region called the oral disk. This adaptation is thought to lessen the energetic cost of feeding (Domning, 1976). In contrast, trichechid rostrums are significantly less deflected compared to dugongs and end in a smaller rounded region compared to dugongs. Significant differences in rostrum deflection occur among trichechids (Domning, 1982). Manatee mean rostrum deflections are reported as follows: Amazonian manatees,  $30.4^{\circ}$  (S.D.=3.40), African manatees,  $25.8^{\circ}$  (S.D.=5.73), and West Indian manatees,  $38.2^{\circ}$  (S.D.=4.88) (Domning, 1982). Geographic variation in rostrum deflection occurs within West Indian manatees as follows: South American population,  $33.8^{\circ}$  (S.D.=5.23, N=15), Florida and Gulf Coast population,  $40.1^{\circ}$  (S.D.=5.00, N=35) (Domning, 1982). The differences in rostrum deflection among living sirenians are speculated to be correlated with feeding strategy such that greater deflection is associated with a greater

percentage of time spent bottom-feeding compared to feeding on floating and emergent vegetation (Domning, 1976).

Manatees possess a unique dentition that involves supernumerary teeth where teeth erupt in the rear of the mouth and progress forward as they wear until they are shed at their rostral position. Dugongs possess open rooted, peg-like teeth; only two to three teeth are functional at one time. New molars erupt later in life presumably as an adaptation to tooth wear. Dugongs also possess incisors that erupt as tusks in males but usually remain unerupted in females. Lanyon (1991) hypothesized that dugong teeth are nonfunctional and that mastication of seagrass is accomplished by the upper and lower horny palates. Although the lack of function of dugong teeth has not been proven, it is plausible that the enlarged horny palate plays a large role in processing seagrasses.

Steller's sea cow was an exceptional Recent sirenian. It was reported to be as long as 8 meters and it was estimated to weigh up to ten tons. The length of the head was 1/10 body size and its limbs lacked phalanges. The tail was fluke-shaped. The skin was described as thick and bark-like, presumably an adaptation for living in the near-shore rocky surge. Teeth were absent and were replaced by a horny palate which were used to grind soft kelp (Domning, 1976). The rostrum of Steller's sea cow was only slightly deflection from the horizontal ( $35^{\circ}$  to  $45^{\circ}$ ) compared to dugongs ( $67^{\circ}$  to  $72^{\circ}$ ) (Domning, 1976). This feature of the feeding apparatus enabled Steller's sea cow to feed upon kelp which grew in the inter-tidal and upper subtidal zones.

### Digestive Strategy

All sirenians are non-ruminating, hindgut fermenting herbivores; the gastrointestinal tract of all members of the Order is similar (Lemire, 1968; Marsh *et al.*, 1977; Murray *et al.*, 1977; Reynolds, 1980; Best, 1981; Colares, 1994; Reynolds and Rommel, 1996). Digestion of cellulose occurs with the aid of microbes within a large cecum (Reynolds, 1980; Snipes, 1984; Burn, 1986; Burn and Odell, 1988). Manatees and dugongs possess long gastrointestinal tracts which may reach lengths of 25 to 30 meters (Kenchington, 1972; Spain and Heinsohn, 1975; Murray *et al.*, 1977; Reynolds, 1980; Reynolds and Rommel, 1996). The large and small intestines of the Florida manatee are of equal length; however, the large intestine of the dugong is approximately twice as long as the small intestine (Kamiya and Kataoka, 1979; Reynolds and Rommel, 1996). Gastrointestinal tracts (including digesta) have been reported to account for 10% of body weight in dugongs (Marsh, 1977; Murray *et al.*, 1977) and up to 23% of body weight in Florida manatees (Reynolds and Rommel, 1996). Passage rates for both species are also very long; approximately 145 hours for manatees (Lomolino and Ewel, 1984). Long retention time may be an aquatic adaptation. Digestion efficiency is high in the Florida manatee and the dugong. Lomolino (1977) and Lomolino and Ewel (1984) reported manatee digestion efficiency rates as high as 83 to 91%; such efficiency exceeds ruminants by 10 to 20% (Lomolino, 1977; Best, 1981; Lomolino and Ewel, 1984; Burn, 1986). Dugongs are reported to have high digestion efficiency rates, up to 85% for seagrasses (Murray *et al.*, 1977). However, similar studies in Amazonian manatees reported only 44 to 68% efficiency rate of digestion (Best, 1981). This higher rate of efficiency is likely due to the long rate of passage through the gut which has

been shown to be proportional to the amount of cellulose digestion (Parra, 1978).

Manatees exhibit a low metabolic rate (Gallivan and Best, 1980; Irvine, 1983), 17-22% less than expected based on terrestrial ungulates of comparable body size. Such data are not available for dugongs, but due to similar life histories and low tolerance for cold, it is likely that dugongs also possess a low metabolic rate for their body size (Preen, 1992). The restriction of all extant sirenians to tropical to sub-tropical regions may, in part, be related to low metabolic rate and cold intolerance; Florida manatees and dugongs show sensitivity to water temperatures and will search out warm water during periods of cold weather (Hartman, 1979; Gallivan *et al.*, 1983; Irvine, 1983; Anderson, 1986). Low metabolic rate may also be an adaptation or result of aquatic herbivory (see McNab, 1988). Low metabolic rate may contribute to the slow passage rate of food through the gastrointestinal tract, and to high digestion efficiency (Gallivan and Best, 1980). Higher metabolic rates would cause ingesta to be moved through the intestine too fast to extract enough nutrition to make aquatic herbivory successful on such low quality food. Modification of passage rates will increase digestion efficiency (Burn, 1986). The lower content of fiber and lignin in aquatic vegetation enables sirenians to extract more nutrients despite it being a low quality food source. Terrestrial hind-gut fermenting herbivores could not follow this strategy due to the higher levels of lignin and fiber found in terrestrial plants.

Due to the close relationships among morphology, function and ecology, it is beneficial to have a complete understanding of the ecology of the organism of study. This relationship is particularly true for sirenians; structure of the feeding apparatus has been shown to affect the feeding ecology of sirenians

(Domning, 1976, 1977, 1978, 1980, 1982; Domning and Hayek, 1986). Therefore, I now review the feeding ecology literature for each sirenian species.

### Florida Manatee Feeding Ecology

Several studies have been conducted to examine the foraging ecology of Florida manatees. At one time, manatees were thought to be useful in clearing water-ways of nuisance aquatic vegetation which often makes navigation difficult or impossible. Manatees were used successfully in clearing aquatic vegetation from Georgetown's water purification plant adjacent to the Botanical Gardens in British Guyana (Allsopp, 1961). Manatees are described as "clearing sections of canals systematically and in a methodical fashion." The animals were reported to eat *Eichhornia crassipes* (water hyacinth), *Pistia* (water lettuce), *Nymphaea* (yellow water lily), and other floating vegetation. However, subsequent reports indicate that use of manatees in larger systems was not effective due to problems associated with control of water temperature and the large numbers of individuals needed (Allsopp, 1969).

Campbell and Irvine (1977) reviewed the current knowledge of manatee feeding ecology and future plans of the U.S. Fish and Wildlife Service manatee lab. The only knowledge at that time was the potential for manatees to control aquatic vegetation (Allsopp, 1961, 1969) and Hartman's (1971) dissertation on manatees in Crystal River, Florida.

Hartman (1979) discussed the foraging ecology and feeding habits of the Florida manatee in the Crystal River region. Manatees were described as "opportunistic feeders," likely to select plants based on palatability, digestibility, and nutritional value. Hartman reported that manatees seem to prefer submerged vegetation to floating vegetation. In impoverished areas of

vegetation, manatees may supplement their diet with several species of algae (Hartman, 1979). However, generally manatees were "relatively indiscriminant" and ate most submerged vegetation that they encountered (Hartman, 1979). Hartman (1979) reported that in the Crystal, Homosassa, and Withlacoochee rivers, manatees fed primarily on *Hydrilla verticillata* (Hydrilla), *Vallisneria neotropicalis* (water celery), *Ceratophyllum demersum* (coon-tail), *Myriophyllum spicatum* (Eurasian water milfoil), *Ruppia maritima* (widgeon grass), and *Diplanthera wrightii* (shoal grass, now named *Halodule wrightii*). Manatees consumed large quantities of *Hydrilla verticillata*, but this does not necessarily reflect a preference due to the abundance of Hydrilla. However, in areas where only *Ceratophyllum demersum* and *Myriophyllum spicatum* grew, manatees showed a preference for *Ceratophyllum*. Hartman (1979) also pointed out that manatees preferred *Ruppia maritima* to *Myriophyllum spicatum*. In marine environments, manatees fed on *Syringodium filiforme*, *Thalassia testudinum*, and *Diplanthera wrightii* but seemed to prefer *Syringodium filiforme* where it grew mixed with *Thalassia testudinum*.

Manatees at Blue Spring Run on the St. John's River (Volusia County) were observed feeding upon *Eichhornia crassipes* (water hyacinth) (Hartman, 1979). Individuals would approach these plants from below, grasp the plant by "evert[ing] their lip pads" and pull the plant under water. Manatees often submerged to the bottom to feed upon these plants, which they held with both flippers and ate leaf by leaf. Usually stalks and roots were not eaten, but some individuals would consume the entire plant. When feeding upon the seagrasses *Thalassia*, *Syringodium*, *Diplanthera* (*Halodule*), and the brackish vascular plant *Ruppia*, manatees ate only the leaves. However, when feeding upon *Vallisneria*, bases of leaves, leaf shoots and young tender leaves appeared to

have been preferred. No preferences for young or mature plants were observed for the seagrasses or *Ruppia*. *Hydrilla* was fed upon at the marginal edges or by immersing themselves into the large stands. Often manatees would hollow out small "caves" of *Hydrilla*. *Ceratophyllum* was fed upon in a browsing manner, wherein only the top portions of each plant were taken. Differences in feeding habits with location are reported for manatees occurring in the St. Johns River, Citrus and Volusia (Blue Spring Run) Counties (Hartman, 1979).

Although manatees eat both freshwater and marine algae in captivity, algae does not constitute a significant portion of their diet unless vascular plants are unavailable (Hartman, 1979). At no time were manatees observed feeding upon *Sargassum* or upon marine algae beds. Manatees incidentally ingested epiphytic algae and other organisms encrusted upon the vegetation on which they grazed. *Enteromorpha*, *Spirogyra*, *Claophora*, and *Oscillatoria* were the dominant freshwater encrusting algae. Also, manatees incidentally ingested a large number of encrusting diatoms, red and blue-green algae that encrust many seagrasses such as *Thalassia testudinum*. Many invertebrates in fresh and saltwater are also reported to be consumed. Hartman (1979) listed amphipods, isopods, tiny shrimp, crayfish, crabs, insect larvae, bivalves, snails, leeches, nematodes, platyhelminths, polychaete worms, tunicates, hydroids, byozoans, anemones, and brittle stars as common animals incidentally ingested. Gammarid and caprellid amphipods are very common in vegetation. Hartman (1979) suggested that arthropods occur in large enough abundance as to provide a significant contribution of protein to the diet of manatees. Manatees foraged along the substrate, ingesting detritus, sand and mud. Hartman (1979) suggested that individuals are ingesting trace elements and other minerals to supplement the diet. Manatees were also observed to ingest feces of other manatees.



Manatees fed in short bouts lasting 60 to 90 minutes, although some feeding bouts lasted as long as two hours (Hartman, 1979). Feeding bouts of calves were shorter in duration. The depth at which manatees often fed depended upon the depths of plants. In Crystal River, manatees fed in water as deep as 4 meters. Individuals were never observed to feed upon *Hydrilla* below 4 meters even though it grew at greater depths in the main spring. There are many anecdotal reports that manatee feeding sites are not random but selected. Groups of manatees fed at particular sites regularly, returning to the same site until the resources were depleted or another site became more favorable. Feeding sites may have been seasonal (Hartman, 1979).

Domning (1980) conducted feeding trials with captive manatees to test his earlier hypothesis (Domning, 1976) that it would be advantageous (energetically) for sirenians to keep the body axis close to the horizontal plane. This behavioral difference might account for the difference in rostrum deflection found among sirenians. Rostrum deflection appears to be a result of natural selection acting on the morphology of the feeding apparatus respective of the specific taxon's environment and feeding preferences. For example, Amazonian manatees have the least deflected rostrum of all sirenians. Domning (1977, 1978) speculates that this is due to the fact that *T. inunguis* feeds mostly on natant vegetation. At the other extreme, the dugong (*Dugong dugon*) has the most downturned rostrum because dugongs are specialists on seagrass and always feed on the substrate (Domning, 1976). The rostrum of West Indian and African manatees (*T. manatus* and *T. senegalensis*, respectively) are intermediate between dugongs and Amazonian manatees. These trichechids are generalist feeders and are able to feed anywhere in the water column. Domning's behavioral feeding tests were performed on Florida and Amazonian manatees to determine if a feeding position preference indeed was a part of

each individual's behavioral repertoire. The results of a floating vs. attached vegetation trial showed that *T. inunguis* had a strong preference for plants that can be pulled below the surface; *T. manatus* also showed a similar but weaker preference. The difference between the two species for preference for floating vs. attached vegetation was not significant at the  $p < 0.05$  level but the preference was in the right directions. Domning (1980) concluded that, since Florida manatees have been observed to prefer vegetation lower in the water column, the weaker preference of *T. manatus* for food lower in the food column in this study is also qualitatively consistent.

Best (1981) reported on feeding habits of captive manatees. Caribbean (Antillean) and Amazonian manatees spend 6-8 hours a day feeding and individual feeding bouts range from 30 to 90 minutes (Best, 1981). Daily consumption as a percent of body weight is reported to range from 5 to 13%. Best (1981) listed 45 species of aquatic vegetation and 10 algal species that Caribbean manatees are known to eat over their range. Amazonian manatees and West African manatees are reported to feed upon 24 and 8 species of aquatic vegetation, respectively. Coprophagy was reported to be frequent and was thought to be related to the abundant B-complex vitamins and other proteins which are characteristic of herbivore feces.

Packard (1981) examined brackish estuaries and inland waterways on the east coast of Florida. The Intracoastal Waterway between St. Lucie Inlet, Martin County and Palm Beach Inlet, Palm Beach County has long been recognized as important manatee habitat. Large numbers of manatees congregated at the Riveria power plant during the winter (Irvine and Campbell, 1978; Packard, 1981) and currently still do (Reynolds and Wilcox, 1985, 1986, 1994). Seagrass beds in the adjacent Hobe Sound National Wildlife Refuge provide an important source of food for over-wintering manatees in this region. Packard (1981)

reported on manatee abundance, seagrass bed distribution and use by manatees, as well as management recommendations for the region. A mean of 121 different manatees used this area during the winters of 1976 through 1981. Seagrasses in the Intracoastal Waterway from Jupiter Inlet to St. Lucie Inlet was a major resource used by manatees. Known individuals were tracked moving back and forth from the warm water effluent of the power plant to these seagrass beds. Packard (1981) reported that the Hobe Sound seagrass beds (as determined from aerial transect, ground surveys and transect sampling) consisted of 66% *Halodule wrightii* and 28% *Syringodium filiforme*. Six species of marine alga were present (*Halimeda tuna*, *Caulerpa sertularioides*, drift alga-species unknown, *Gracilaria* sp, *Udotea flabellum*, and *Penniculus captiatus*) as well as some *Halophila* sp. and one small patch of *Thalassia testudinum*. The majority of the biomass (50-70%) of *Halodule wrightii* and *Syringodium filiforme* is below ground. Packard (1981) reported that *Syringodium filiforme* provided more available biomass than *Halodule wrightii* and was more prevalent. In addition, Packard (1981) speculated that foraging time would be energetically maximized by rooting and harvesting rhizomes of these seagrasses.

Reynolds (1981) reported on the feeding habits of manatees in southeast Florida. Blue Lagoon is a man-made lake approximately 68 hectares in area that was once open to the Miami river until 1965-66. At that time the South Florida Water Management District installed salinity intrusion barriers at the eastern and western ends of the lake, thereby accidentally trapping the manatees. Later, in May 1976, an automatic flood control system was installed and the manatees were able to leave. This situation allowed Reynolds to study wild manatees in a semi-captive environment. This report was important because it augmented data on manatees by using a year-round population. Reynolds

(1981) reported that manatees appeared to eat aquatic vegetation in the following order of preference: submerged, floating and emergent. These findings corroborate those of Hartman (1979). Submerged vegetation was eaten 77% of the time and included *Hydrilla verticillata*, *Ceratophyllum demersum*. Consumption of algae, *Mougeotia* and *Spirogyra*, was also reported. Consumption of floating vegetation (*Eichhornia crassipes*, *Alternanthera philoxeroides* and *Salvinia rotundiflora*) accounted for 14% of manatee activity. Floating plants were either eaten at the surface or pulled below and consumed. Consumption of emergent vegetation occurred 9% of the time; *Panicum hemitomon* and *P. communis* were observed to be consumed.

Bengtson (1983) presented several species of native vegetation (*Eichhornia crassipes*, *Pistia stratiotes* and *Vallisneria americana*) to wild manatees at Blue Spring Run (St. Johns River, Volusia County, FL) and observed free ranging manatees feeding. Using a hydrophone, Bengtson was able to monitor chewing rates. Using these data, time budgets and feeding curves were constructed. Manatees fed a mean of 5.1 hours per day and consumed 108 grams of vegetation per minute. Bengtson reported a pooled mean chew rate of 1.08 chews per second. Manatees in Blue Spring Run consumed 4 to 9% of their body weight per day. This range is due to the considerable variance of time budgets throughout the year.

A brief report by Lewis *et al.* (1984) documented consumption of algae by manatees over-wintering in Tampa Bay. Four to six manatees were observed feeding in a region that is visited by manatees frequently. In one instance, an individual raised its head above the water line and revealed green algae in its mouth. During a second trip to the area, several sampling quadrats were thrown in the water at randomly chosen locations. All quadrants consisted of marine algae only. *Gracilaria* was the dominant algae (95.1%) followed by *Ulva* sp.

(4.8%) and *Chaetomorpha linum* (0.1%). During this time period in Tampa Bay, seagrass meadows were reported to be decimated by water pollution (Lewis and Phillips, 1980). This report acknowledged that marine algae may be an important source of food for manatees over-wintering in Tampa Bay and supported Hartman's (1979) claim that manatees often supplement their diet with algae as needed.

Packard (1984) commented on the impact of Florida manatees on seagrasses in eastern Florida. Manatees rooted and grazed in seagrass beds. During rooting behavior, manatees consumed entire plants, whereas grazing involved only the blades. Of the total number of seagrass beds in the Jupiter Sound, manatees disturbed 40%. Areas not disturbed were either too shallow (< 50 cm) or were used heavily by fishermen. Packard (1984) estimated that 93 to 96% of seagrass biomass was removed in areas where manatees rooted. Manatee grazing is predicted to change the composition of seagrass beds where rooting behavior occurs. *Thalassia* beds that are stripped of rhizomes are colonized by *Syringodium filiforme* and *Halodule wrightii*. Therefore, manatee grazing would help to increase biodiversity and maintain succession of seagrass beds by giving colonizing species opportunity to spread.

Etheridge *et al.* (1985) examined consumption of aquatic plants by Florida manatees in captivity and at Crystal River, FL. This study differs from Bengtson's (1983) in that consumption rates of *Hydrilla verticillata* were measured. Also, Etheridge *et al.* (1985) adjusted consumption rates based on body size whereas Bengtson (1983) used a mean consumption rate for the sample in that study and did not incorporate body size. Etheridge *et al.* (1985) reported a pooled mean of 1.86 chews per second and significant increases in mean chewing rates for individuals with smaller body size. Mean chew rates between captive and free-ranging manatees were similar. In addition, the mean number

of chews required to consume *Hydrilla* varied inversely with body weight. Etheridge *et al.* (1985) attributed this difference to the fact that calves must chew faster than adults to consume the same amount of food. One captive manatee was fed *Vallisneria* which required many more chews per unit time to consume than *Hydrilla*. Feeding bouts of free-ranging animals ranged from 60 to 370 minutes. Daily consumption rate calculations were based on a 5 hour feeding bout estimate and expressed as percent of body weight. Daily consumption estimates for animals feeding on *Hydrilla* were 15.7% for a calf ( $\leq 175$  cm), 9.6% for a juvenile (176-275 cm), and 7.1% for an adult ( $> 275$  cm). Etheridge *et al.* (1985) pointed out the feeding time is not equivalent to chewing time since feeding time includes time spent moving to new patches of vegetation as well as time spent manipulating plants.

Ledder (1986) reported on the diet of Florida manatees in south Florida. She quantified stomach and gastrointestinal (GI) tract contents using microhistological analysis which is a technique widely used to determine diets of herbivores (Baumgartner and Martin, 1939; Dusi, 1949; Martin, 1954; Croker, 1959; Ward, 1960; Stewart, 1967; Vaughn, 1967; Sparks, 1968; Voth and Black, 1973; Heinsohn and Birch, 1972; Marsh *et al.*, 1982; Hurst and Beck, 1988). The technique identifies species by characteristics of their epidermal cells such as cell size and shape, stomatal characteristics and presence or absence of trichosomes. Manatees in south Florida were found to consume 61 species of vegetation in this study (Ledder, 1986). Occasional consumption of non-plant material including monofilament line and cellophane occurred. Terrestrial grasses were found in 47.6% of the samples. Seagrasses, brackish plants, and freshwater plants were found in 39.3%, 44%, and 16.7% of the sample, respectively. Manatees from south Florida had a diet similar to manatees in the northern counties but different from animals in the central portion of the

state; central Florida manatees consumed a higher percentage of freshwater vegetation as well as a higher percentage of terrestrial grasses (Ledder, 1986). In south Florida, *Halodule wrightii* was consumed the most (24.4%) followed by *Hydrilla verticillata* (12.7%). The third most consumed vegetation was *Syringodium filiforme* (9.1%) followed by *Ruppia maritima* (7.4%), algae (6%), mangrove (5.9%), *Anicum hemitomon* (5.8%), and unidentified terrestrial grasses (5.7%). All other vegetation consumed contributed less than 5% of the diet. Ledder (1986) reported seasonal differences as did Bengtson (1983). Manatees in south Florida consumed *Halodule wrightii* the most in summer and winter months but *Syringodium filiforme* and *Ruppia maritima* in the winter and spring months. *Thalassia testudinum* was consumed more in the spring. Overall, the diet of manatees in south Florida was comprised of 69.2% submerged vegetation, 14.9% emergent and terrestrial vegetation and 0.8% floating plants. Differences between sexes in consumption of the most common species of vegetation were not found.

A brief report by Baugh *et al.* (1989) supports Ledder's (1986) finding that manatees often consume emergent vegetation. Manatees are present throughout the year in Cumberland Sound, Georgia. Manatees fed extensively upon *Spartina alterniflora* (cordgrass). Animals concentrated on the shoots and sheared them off cleanly. Often one to two thirds of individual plants remained. Manatees were not observed to feed upon any other emergent vegetation. However, *Spartina alterniflora* characteristically colonizes low portions of salt marshes and may have been the only emergent available. Baugh *et al.* (1989) stated that *Spartina* may be an important food source for manatees overwintering in the region.

Lefebvre and Powell (1990) observed manatees feeding in Hobe and Jupiter Sounds (central east coast, Florida). Feeding sites indicated that

manatees preferred *Halodule wrightii* in Hobe Sound but no preference was found in Jupiter Sound. The mean water depth of both regions was 0.9 meters and ranged from 0.4 to 1.6 meters. Direct observations of seagrass beds revealed both grazing and rooting behavior. Biomass cores of grazed and ungrazed seagrass beds were taken for *Halodule wrightii*, *Thalassia testudinum* and *Syringodium filiforme*. The number of shoots, as well as shoot and rhizome biomass removed in the grazed vs. ungrazed areas were significantly different except for shoot count of *Thalassia*. Only shoot biomass and rhizome biomass removal of *Thalassia testudinum* was significantly different from ungrazed samples. Lefebvre and Powell (1990) stated that Hobe Sound may be more important to manatees than Jupiter Sound during a milder winter (as was the case for the winter of 1988 and 1989). Hobe Sound has certain advantages if water temperature is not critical. Hobe Sound offers less boat traffic, more accessible seagrass beds further from the main boat channel, and more resting areas for other activities. However, during cold winters, Jupiter Sound is more advantageous due to its proximity to warm water effluents (Packard, 1981). Manatees fed in the winter of 1988-89 in similar locations to the winter of 1987-1988. This finding supports the contention that the same manatees often return to the same familiar grazing sites. Manatees are able to harvest more roots and rhizomes from *Syringodium* than from *Halodule*. Data from the 1987-88 winter and 1988-89 winter both show greater harvesting of *Syringodium* root and rhizome (58.8% vs 48.1% and 66.7% vs. 46.2%, respectively). It is still unknown whether manatees consume roots and rhizome of *Thalassia testudinum*. Lefebvre and Powell (1990) clearly stated that their results do not show any short-term negative impact on seagrass bed re-growth caused by manatee grazing, although there were a few sites where re-growth may have been negatively impacted. Problems of seagrass re-growth in these areas were due to



marginal conditions of seagrass where grazing effects were mixed with environmental factors that reduced re-growth.

Provancha and Hall (1991) described manatees feeding on seagrass beds in the Cape Canaveral area. The effects of manatees on seagrasses were observed as part of a long term ecological monitoring program. Manatees are common in the Banana River near the Kennedy Space center from spring until fall. Large numbers of manatees (200 to 300) began using the area between 1985 and 1987. A preferred area to feed in these years was a large seagrass meadow dominated by *Syringodium filiforme*. This site provided many opportunities to observe manatees feeding. This study differed from others in that it attempted to quantify the effects of free-ranging manatees by use of exclusion cages. The area is restricted and therefore essentially a manatee sanctuary which is not populated by other large marine herbivores (e.g., green turtles, *Chelonia mydas*). Provancha and Hall (1991) reported large changes in the submerged aquatic vegetation (SAV) population. Original blade heights of enclosed SAV ranged from 18 to 29 cm before they were enclosed. Post-grazing height of enclosed SAV increased to a range of 25 to 31 cm. Outside the enclosures the range of blade height was reported to be 5 to 9 cm. The density of *Syringodium* inside the enclosure showed no change. However, *Syringodium* density outside the enclosures was significantly reduced. There is some evidence that *Halodule wrightii* may have replaced the *Syringodium* which was grazed. Aerial surveys of manatees showed a positive correlation of manatee distribution with *Syringodium* and *Halodule* beds and a negative correlation with *Caulerpa*, a marine alga. *Halodule* showed a negative correlation with increasing depth of water. The results of this study show that usually *Syringodium* and *Halodule* do not occur with *Caulerpa* in this study area. Of the three types of aquatic vegetation, *Syringodium* has the lowest

percentages of protein, fat and fiber but also the highest percentages of carbohydrate and potassium (mg/g). Manatees appeared to crop the blades just above the meristem with little evidence of rooting present. These results differ from those of Packard (1981), who report extensive rooting behavior. This difference may be related to the fact that manatees in the Packard (1981) study were over-wintering and perhaps needed additional calories. It is also possible that the nutritional quality of seagrasses declines during the winter months. This possibility was also suggested by Bengtson (1983) for freshwater vegetation. Provanča and Hall (1991) suggested that manatees were actively selecting *Syringodium* and avoiding *Caulerpa*, although these authors recognized that if the two types of vegetation do not occur together then the possibility exists that manatees do not encounter *Caulerpa*. Effects of grazing on seagrasses are not known. However, this study speculates that herbivory may be advantageous to seagrass beds by aiding in dispersing plant fragments and increasing nutrients available from manatee feces. There is some evidence that grazing could enhance the nutritional content of seagrasses (Thayer *et al.*, 1984). Bjorndal (1980) reports that green sea turtles maintain grazed areas of *Thalassia testudinum* and nitrogen content in these plots was higher than in non-grazed plots. Consumption rates of manatees feeding on *Syringodium* were calculated using Packard's (1981) 1 gram wet weight to 0.18 g dry weight conversion and Bengtson's (1983) calculation that manatees consume 33.2 kg/day. Provanča and Hall (1991) estimated that manatees fed on 5.9 kg/day (dry weight). Taking in account that seagrass in this study had a biomass value of 131 grams/m<sup>2</sup>, manatees in this study are estimated to have fed on a total of 45.6 m<sup>2</sup> of seagrass per day per manatee. The total study area (1,755,000 m<sup>2</sup>) was divided by the value 45.6 m<sup>2</sup> of seagrass per day which yielded 38, 486 days in the study. This value, divided by the total number of manatees in study (206,

maximum count) yielded approximately 186 days of grazing available for each manatee. However, a large percentage of manatees migrate away from the study site after 60 days; only 30% of the biomass was actually consumed. During this time, seagrass resources were not depleted and were rapidly replaced. It appeared that at this study site, manatee grazing effects on seagrass recruitment were minimal at best.

### Amazonian Manatee Feeding Ecology

Amazonian manatees feed approximately six to eight hours a day (Best, 1981). They feed only upon freshwater species of aquatic plants and grasses. The availability of plants is seasonal and dependent upon the annual wet season, during which time water levels may rise ten to fifteen meters (Best, 1981). River and lake waters rise and inundate flood-plains, resulting in increased production of aquatic and semi-aquatic plants and grasses (Best, 1981). This phenomenon allows manatees to range further than during the dry season and consume a greater number of species of floating plants. Reported natural foods of *T. inunguis* are listed in Appendix B. During the dry season, river and lake levels shrink, floating meadows that are characteristic of this habitat become dormant or die and decompose (Junk, 1970; Best, 1981). During these times, food is scarce and manatees are observed feeding on the rotting stalks of floating plants and mud, potentially to obtain minerals (Best, 1981). Such seasonality in food availability may be responsible for the observed seasonality of breeding in Amazonian manatees (Best, 1981, 1982, 1983, Marmontel *et al.*, 1992). Best (1981) reported that manatees feeding upon *Pistia stratiotes* ate the leaves and roots but left the center core, which is dense, untouched. When feeding upon grass

(*Panicum purpurascens*) only the leaves were consumed. However, *Cabomba* sp. was entirely eaten.

#### West African Manatee Feeding Ecology

Only incidental observations have been made on the feeding habits of West African manatees. However, due to similarities in life histories and habitats, it is likely that observations made for West Indian manatees may be extrapolated to *T. senegalensis*. Vascular plants of the coasts and rivers of west Africa offers resources for West African manatees. Where submerged or floating vegetation is absent, manatees may feed upon emergent vegetation and mangroves (*Rhizophora*)(Best, 1981). Some stomach content samples have shown that *T. senegalensis* occasionally feeds on clams; this has also been reported for West Indian manatees near Puerto Rico (Reynolds and Odell, 1991). Appendix C summarizes plant species known to be consumed by West African manatees.

#### Dugong Feeding Ecology

Dugongs are seagrass specialists. They feed almost exclusively upon Potamogetonacean and Hydrocharitacean seagrasses (Bertram and Bertram, 1968; Kingdon, 1971; Heinsohn and Birch, 1972; Lipkin, 1975; Heinsohn *et al.*, 1977; Marsh *et al.*, 1982). The following genera are consumed by dugongs in northern Queensland: *Cymodocea*, *Enhalus*, *Halodule*, *Halophila*, *Syringodium*, *Thalassia*, *Thalassodendrin* and *Zostera* (Johnstone and Hudson, 1981; Marsh *et al.*, 1982). Dugongs in Shark Bay (western Australia) feed extensively over *Amphibolis antarctica* meadows (Anderson, 1986). Dugongs have been reported

to feed upon marine algae if seagrasses are not available (e.g., during cyclone events) but usually the occurrence of algae in stomach contents is low (Spain and Heinsohn, 1973; Heinsohn and Spain, 1974; Marsh *et al.*, 1982). Macro-invertebrates have been found in the stomach contents of several dugongs (Pfeffer, 1963; Spain and Heinsohn, 1973; Lipkin, 1975). Anderson (1989) and Preen (1995) report that dugongs at the southern extent of their range in Australia, east coast and west coast respectively, deliberately forage on macro-invertebrates such as ascidians and polychaetes, possibly to supplement their diet with protein.

Preen (1992) reported that in Moreton Bay, which is in the subtropical range, dugongs prefer to feed upon small, tender and low fiber species of seagrasses such as *Halophila* rather than *Zostera*. When dugongs did feed upon *Zostera*, they fed only upon the thin leaf form (rather than the broad leaf form) and then only consumed the leaves instead of the entire plant (including rhizomes). Additionally, dugongs in the subtropical environment forage in herds and appear to display high site fidelity, returning to the same seagrass meadows. Site fidelity has been interpreted as cultivation of seagrasses. Constant grazing of seagrasses creates new growth and maintains pioneer species which dugongs seem to prefer. New growth is lower in fiber and lignin and, therefore, digestion is easier and more efficient (Thayer *et al.*, 1984; Preen, 1992).

When comparing the feeding ecology of manatees and dugongs, one striking difference is the feeding trails made by dugongs. Dugongs feed preferentially upon small, low fiber species of seagrasses (Lanyon, 1991; Preen, 1992). When feeding upon such seagrasses, the entire plant is excavated from the substrate and both leaves and rhizomes are ingested. These feeding trails range from 19 to 25 cm wide, 3 to 5 cm deep, and may be up to 8 meters long

(Anderson and Birtles, 1978; Heinsohn *et al.*, 1977). Up to 86% of the biomass has been found to be removed along these feeding trails (Heinsohn *et al.*, 1977).

### Steller's Sea Cow Feeding Ecology

Although Steller's sea cow is now extinct, Steller (1899, 1925) documented his observations on the natural history of this sirenian. *H. gigas* was restricted to the cold waters of the Bering Sea where it fed on marine algae (kelp) and possibly seagrasses such as *Phyllospadix* sp (Steller, 1899, 1925; Domning, 1976). Steller reported that animals would walk into the shallows with their reduced limbs which they also used to "dig out and tear off the algae and seagrass from the rocks as a horse would do with its front teeth". The animals would move their heads and necks, apparently underwater, like oxen while eating. They would lift their heads every few minutes to breathe. Steller (1899) reported a preference for several species of Phaeophytes and Rhodophytes but consumption of all types of seaweeds occurred. Appendix D summarizes foods eaten by *H. gigas*.

### Significance

Several studies have examined the anatomy, behavior and ecology of sirenians. However there are still large gaps in our knowledge of the natural history of manatees and dugongs; much more work needs to be done. Anatomical examinations, to date, should be considered as the groundwork for future studies. There are many references to the perioral bristles of feeding manatees but the descriptions are often brief and anecdotal. Perioral bristles in dugongs are mentioned even less. A systematic study of the anatomy of the

perioral bristles, associated structures, and their use during feeding in both manatees and dugongs has not been completed at this time. Ecological studies have focused upon what species of vegetation manatees eat and how manatees impact seagrasses. Although some work has been done regarding consumption rates, these studies were limited in the variety of aquatic plants used and none incorporated seagrasses into their experimental design. This is an important consideration since manatees are generalist feeders that may consume over 60 species of aquatic plants. Many questions regarding consumption of vegetation still remain unanswered. Studies which integrate both morphology and ecology are fewer still. Some evidence exists which suggest the degree of deflection of the rostrum in trichechids affects preference among floating, emergent, and submerged vegetation. However, such questions beg to be addressed more completely. Rhizophory is an important component of sirenian feeding ecology; however, it is still unclear as to how manatees (and dugongs) excavate rhizomes. This dissertation seeks to bridge this gap in sirenian natural history and integrate anatomical and behavioral data to aid in understanding the foraging ecology of sirenians.

### Organization of the Dissertation

This dissertation describes the morphology of the sirenian rostrum and feeding apparatus, and explains the behavioral use of this feeding apparatus with respect to foraging and interaction with the environment and conspecifics. Specifically, the objectives of this dissertation are as follows:

1. To characterize the anatomy of perioral bristles and other specialized hairs of the rostrum of Florida manatees by mapping their distribution, morphologies, densities and gross innervation (Chapter 2).

2. To examine the behavioral use of perioral bristles and other specialized hairs of the rostrum of Florida manatees during feeding (Chapter 3).
3. To examine the behavioral use of perioral bristles and other specialized hairs of the rostrum of the Florida manatee during non-feeding, tactile activities and to determine the range of behavioral flexibility of which the organism is capable (Chapter 3).
4. To characterize the facial muscles of Florida manatees and elucidate the mechanism of perioral bristle protrusion and movement in Florida manatees (Chapter 3).
5. To propose a functional model which integrates both anatomy and behavior to explain the observed range of behaviors involving the perioral bristles of Florida manatees (Chapter 4).
6. To elucidate, experimentally, differences in manipulation and rates of consumption by Florida manatees feeding on different species of aquatic vegetation normally consumed in the wild (Chapter 5).
7. To examine the behavioral use of perioral bristles and other specialized hairs of the dugong, Amazonian manatee, and the Antillean manatee rostrum during feeding and tactile activities (Chapter 6).
8. To integrate these findings and propose hypotheses regarding convergence of form, function and ecology of benthic foraging marine mammals and their integral place within a spectrum of vibrissal use in all mammals (Chapter 7).



CHAPTER 2  
DISTRIBUTION AND INNERVATION OF FACIAL BRISTLES  
AND HAIRS IN THE FLORIDA MANATEE (*Trichechus manatus latirostris*)

Introduction

Sirenians have evolved specialized orofacial anatomies which serve their unique role as mammalian aquatic herbivores. Notable in manatees are the large fleshy upper lips containing stiff bristles (Vrolik, 1852; Murie, 1872; Chapman, 1875; Murie, 1880; Garrod, 1879; Mohr, 1957) which are modified vibrissae that are actively everted and used in a prehensile grasping fashion during ingestion of plants and manipulation of inanimate objects (Chapman, 1875; Garrod, 1879; Murie, 1880; Hartman, 1979; Marshall and Reep, 1994, 1995b, 1995c; Marshall *et al.*, 1995, 1996). Other bristle fields are present in discrete locations distributed around the perioral region; all play a role in manipulating vegetation during feeding behavior (Chapter 3). Bristle-like hairs (which are intermediate in stiffness and morphology between perioral bristles and body hair) densely cover the anterior-most portion of the rostrum called the oral disk. The thinner body hair is more sparsely distributed on the remainder of the body. The face, particularly the oral disk, is brought into contact with plants, conspecifics, and other objects during the frequent tactile exploratory behavior of manatees, and is quite sensitive to human touch (Hartman 1979, Marshall *et al.*, 1996).

Sirenians, some rodents and marsupials possess discrete clusters of specialized neural aggregations in specific areas of the cerebral cortex (Dexler, 1913; Marshall and Reep, 1995a; Reep *et al.*, 1989; Welker, 1971; Welker and

Woolsey, 1974; Weller, 1972, 1993; Woolsey and Van der Loos, 1970). These structures are best known in mice and rats where they occur as "barrels" in layer IV of somatosensory cortex. Electrophysiological studies have shown that each mouse "barrel" processes information from a single vibrissa (Woolsey and Van der Loos, 1970; Woolsey *et al.*, 1975; Van der Loos, 1976). Furthermore, the spatial distribution of "barrels" and related neural aggregations in the trigeminal brainstem and thalamus, mimic the pattern and arrangement of the mystacial vibrissae (Woolsey, 1967; Ma and Woolsey, 1984; Ma, 1991). Similar mapping of barrels and mystacial vibrissae has been demonstrated in the brush-tailed possum (*Trichosurus vulpecula*) and tammar wallaby (*Macropus eugenii*) (Waite *et al.*, 1991; Weller, 1972, 1993). However, the brush-tailed possum possesses neural aggregations in layer IV that have a solid center, in contrast to the hollow barrels of mice and rats (Weller, 1972, 1993). Florida manatees and dugongs possess neural aggregations (termed Rindenkerne) similar to "barrels" in the presumed facial region of somatosensory cortex (Dexler, 1913; Reep *et al.*, 1989; Marshall and Reep, 1995a). Rindenkerne are also solid, as in brushed-tail possums, but are located in cortical layer VI rather than layer IV. They share histochemical attributes with the barrels of mice and rats in that they stain positive for cytochrome oxidase and acetylcholinesterase (Reep *et al.*, 1989; Marshall and Reep, 1995a). In addition, the number of the largest class of Rindenkerne is approximately equal to the number of mystacial vibrissae (this chapter). Although circumstantial, the evidence supports the hypothesis that neural aggregations in somatic sensory cortex of some taxa with well developed vibrissae are involved in processing information from vibrissae. The distribution, density, morphology, and gross innervation of perioral bristles and tactile hairs of the rostrum have been mapped and identified in Florida manatees. Such data have become an integral part of the development

of a functional model of feeding behavior (Marshall *et al.*, 1996). In addition, quantification of perioral bristles provides a basis for testing the hypothesis that each tactile bristle and hair is represented by a corresponding cluster of neurons (Rindenkern) in the somatic sensory region of cerebral cortex (Reep *et al.*, 1989; Loerzel and Reep, 1991; Marshall and Reep, 1995a).

## Methods

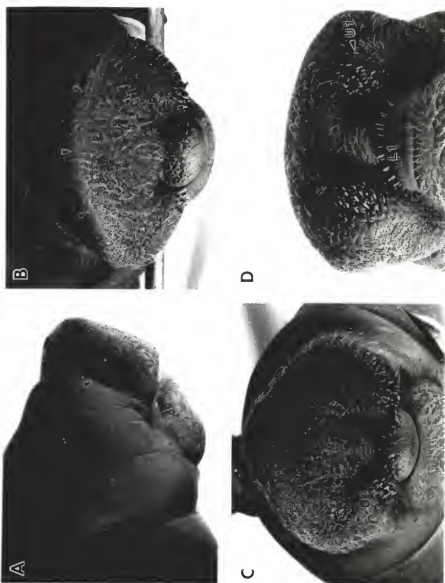
### Bristle and Hair Distribution

Postmortem heads of 27 Florida manatees were obtained within 48 hours of death under permit PRT-684532, through the statewide salvage and necropsy program, administered by the Florida Department of Environmental Protection. All specimens were selected on the basis of good general body condition and suitability for taking histological samples. Body weights and lengths (Florida Department of Environmental Protection data) were recorded for most of the specimens. Perioral bristles were counted on both sides of the face on 12 specimens, within each of the six fields identified. Bristle counts were made bilaterally within a subset of the six fields on 15 specimens. Bristle-like hair counts were made on 17 specimens. The region of the face on which hair counts were made was limited to the maxilla region and extended from the anterior-most extent of the rostrum (the oral disk) to the post-nasal crease (Figure 2). A rectilinear grid was drawn over the orofacial region. A ridge of tissue or transition zone between the soft, supple region of the oral disk and the firmer upper rostrum was used as a landmark (Figure 2). This landmark will be referred to as the "orofacial ridge." The orofacial ridge demarcated the x-axis of a grid covering the facial region. Therefore the oral disk was ventral to the x-

axis and the supradisk region dorsal and caudal to it. The y-axis represented the midline of the long axis of the head. The ventrolateral angles of the upper lips represented the lateral boundaries (the upper bristle pad lies medial to this boundary). The region described above was marked in a rectilinear grid of 2x2 cm squares, and total face area was approximated as  $4 * (\# \text{ squares}) \text{ cm}^2$ . All hairs were counted in each grid square and the number entered on a standardized schematic map of the face. Each hair was cut or plucked to ensure that none was counted twice. Two areas not included in the grid maps due to curvature were the ventral angle of the upper lip in the supradisk region, and the corresponding portion of the oral disk which lies immediately lateral to the U2 bristle field. Hairs in these two areas were counted as lumped values, and were used in total count computations but not in density calculations. Counts and densities were computed for each quadrant (left upper, right upper, left lower, right lower) and hemispace (left/right, upper/lower). Chin hairs were counted and their lengths measured on 13 specimens. No delineation of left or right boundaries was made for these measurements. The chin was defined as the anterior-most region of the lower jaw covered with darkly pigmented epidermis (compared to the lightly pigmented lower fields) caudoventral to the angle between the upper and lower lips dorsally and a large crease ventrally (Figure 2).

Statistical analysis was done using Statview, and greyscale maps were generated using Spyglass, on a Macintosh computer. Probability values given are for paired t-tests, and  $r^2$  values are for linear regressions, unless otherwise noted.

Figure 2. Photographs of a postmortem fetal manatee (SWFTM 8618F). In the lateral view of A, the prominent postnasal crease (arrow) indicates the caudal boundary of the supradisk region. Note the abundance of facial hair compared to the postcranial body. Panels B-D represent progressively more ventral views of the same individual. In B the orofacial ridge (arrows) demarcates the boundary between the oral disk and supradisk region. In view C the oral disk is seen face on, and the U2 bristle group is prominent. In panel D the L1 bristles are everted (compare with Figure 4).



### Innervation

Three postmortem heads were perfused and immersed in 4% paraformaldehyde and kept in this solution throughout the procedure. The epidermis was removed from the first specimen using a number 10 scalpel blade and tissue forceps. Sub-dermal fat and connective tissue were removed from the upper jaw, revealing superficial nerve branches and facial musculature. Nerve fibers were traced into both superficial and deep facial musculature using blunt dissection. Nerves on the upper jaw were traced from point of exit from the skull to their termination on either sensory structures or in facial musculature. Skin, dermal fat and connective tissue were then removed from the lower jaw of the second cranial specimen. Superficial nerve branches were traced to their termination within facial muscles. Deeper musculature was then removed to reveal the mandible. Using bone forceps, the mandible was cut and nerve branches were traced along the medial surface of the bone to their point of exit rostrally. These branches were then followed to their terminations in the follicular capsules of facial bristles of the lower jaw. Identical procedures were carried out on both the upper and lower jaws of the third specimen.

### Results

#### Distribution of Perioral Bristles

The face of Florida manatees is comprised of five regions: the oral disk, supradisk, chin, and upper and lower bristle pads (Figs. 2-4). The oral disk is the region situated between the mouth and orofacial ridge, and is continuous ventrally with the U1 and U2 bristle fields. The orofacial ridge is a ridge of hard

tissue which serves to separate the soft, supple region of the oral disk from the firmer supradisk (Figure 2). This supradisk region extends caudally to a deep crease which I refer to as the "postnasal crease." This landmark is positioned caudal to the nares but rostral to the orbits. I have identified six groups of perioral bristles, four on the upper lip (U1-U4) surrounding the boundary of the oral cavity, and two on the lower lip (L1-L2) also surrounding the boundary of the oral cavity (Figure 3). They are easily distinguished from hairs and bristle-like hairs by their larger diameter and greater stiffness. The locations of these distinct fields are shown in Figures 2 through 5. Counts, lengths and diameters of bristles are given in Tables 1 and 2. Each bristle field contains a relatively constant number of bristles of a characteristic diameter and length. There were no significant differences between counts from the left and right sides for any of the six bristle fields.

The four groups of upper bristles form a contiguous "bristle pad" located medial to the ventrolateral angle of the lip (Figs. 2, 3). The most prominent bristles are those in the U2 group, which consists of about 23 long thick bristles per side of the upper lip, organized in a circular array (Figure 2 C, D). They are usually retracted within skin folds, then everted during manipulative behaviors (see Chapter 3). These bristles are about 2 mm in diameter and 5-10 mm in length, depending on whether they are everted. The U1 bristles are distinct from the U2 group and noticeably thinner, though of comparable length (Figure 2D). Group U3 is a triangular field of short stout bristles arranged in rows, and is located caudal to the U2 bristles along the medial to the ventrolateral angle of the upper lip (Figure 4). Bristle group U4 extends caudally from the apex of the U3 field, and consists of a line of long thin bristles (Figure 4). On the lower lip, groups L1 and L2 also form a contiguous "bristle pad". Bristles of the L2 field consist of short bristles much like those of group



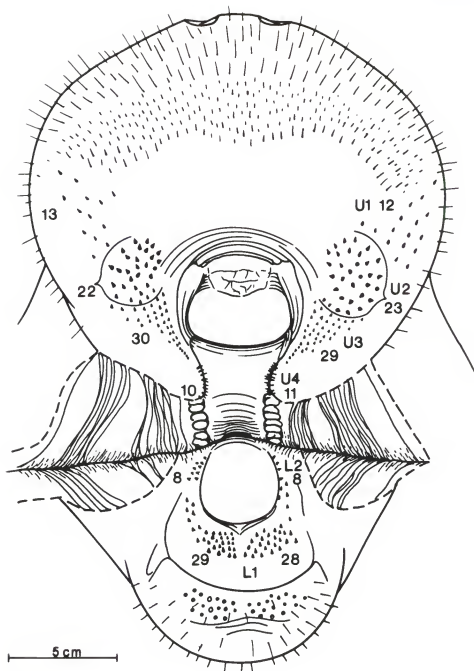


Figure 3. Schematic diagram representation of the bristle fields, with mean counts given for the left and right sides for each bristle field. The bristle-like hairs of the oral disk and the hairs of the supradisk are also visible.

Figure 4. View of the dorsal interior of the oral cavity, lower jaw removed, specimen MSW 215. The extent of the triangular U3 bristle field is indicated by arrows. The U4 bristles are arranged in a single row. Note the upper callous pad (up), palate (pl), and ventrolateral angle of the upper lip (asterisks).

Scale:  2 cm

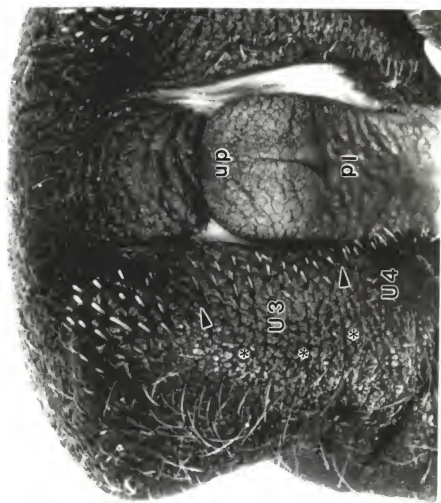



Figure 5. View of the ventral interior of the oral cavity, tongue removed, specimen TM 8904B. The L1 bristles are in their retracted position within mucosal folds of the lower bristle pad. The midline of the pad is demarcated by a prominent furrow (arrow). Note also the semicircular lip furrow (lf), and horny mandibular pad (mp).

Scale:  1 cm

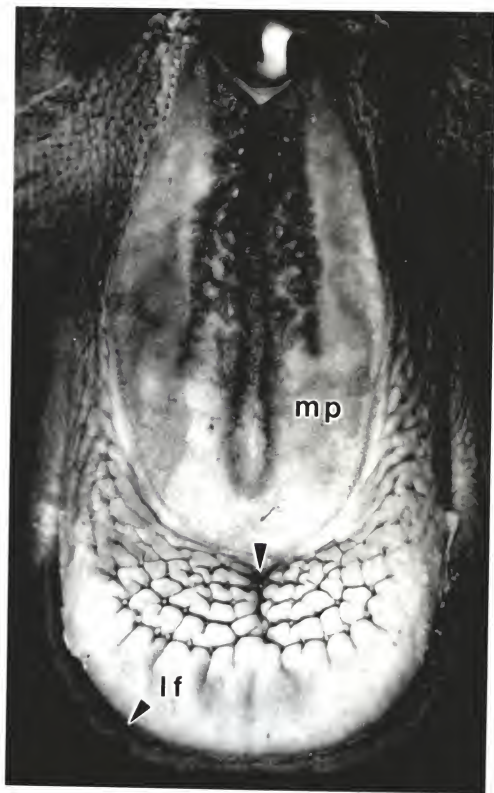


Table 1. Perioral bristles (upper jaw) of the Florida manatee

	<u>U1</u>	<u>U2</u>	<u>U3</u>	<u>U4</u>	<u>U_tot</u>
Mean # per side	12.9	22.7	29.7	10.54	73.1
Standard Dev.	5.9	5.2	8.4	1.4	13.8
Right/Left diff.	0.17	0.22	0.57	0.17	0.42
(p, 2-tailed t test)					
Max. Dia. (mm)	0.8	2.0	0.7	0.5	
Length (mm)	3-7	5(uneverted) 10 (everted)	1-3	2-5	

Table 2. Perioral bristles (lower jaw) of the Florida manatee

	<u>L1</u>	<u>L2</u>	<u>L_tot</u>
Mean # per side	28.5	7.8	36.3
Standard Dev.	5.9	3.9	6.5
Right/Left diff.	0.52	0.99	0.58
(p, 2-tailed t test)			
Max. Dia. (mm)	0.8	0.8	
Length (mm)	1 (uneverted)	1	
	6 (everted)		

U3 (Figs. 2D, 5) The L1 bristles are more robust and similar to the U2 bristles; L1 bristles (Figure 5) are retracted beneath the surface folds of the pad except during manipulative behaviors (see Chapter 3). The L2 group is usually separated from the L1 group, and consists of two rows which extend caudally from the L1 field.

Bristle diameters are greater in adults than in neonates and juveniles. However, bristle counts were similar in adults and neonates; two neonates had the lowest total counts, but one had the highest. The relative distribution of bristles among the six fields was consistent across individuals.

### Distribution of Facial Hairs

The oral disk portion of the face is involved in a flare response seen during phase one of the feeding cycle, and is active during tactile scanning and exploration (see Chapter 3). It contains mostly bristle-like hairs which are intermediate in stiffness between bristles and typical hairs. The supradisk region extends from the orofacial ridge caudally to the post-nasal crease, and contains typical body hairs. The chin contains long body hairs.

There is a mean total of 1722 ( $\pm$  398) hairs on the face (all regions), including 601 ( $\pm$  115) bristle-like hairs in the oral disk region, 710 ( $\pm$  229) body hairs in the supra-disk region, and 411 ( $\pm$ 108) body hairs on the chin (Table 3). There was no right-left difference in total hair number (oral disk plus supradisk;  $p=0.44$ ). Bristle-like hairs on the adult oral disk are 4-6 mm in length, and  $154(\pm 52)$   $\mu$ m in diameter, whereas hairs on the supradisk have lengths in the 5-10 mm range, and diameters of  $94 (\pm 37)$   $\mu$ m. Consistent with their morphology, the hairs of the oral disk look and feel intermediate between body hairs and perioral bristles. Thus, I refer to them as bristle-like hairs. The chin contains long coarse hairs of varying lengths extending up to 18 mm, and having diameters of  $172 (\pm 27)$   $\mu$ m in adults.

Table 3. Total count of facial hair by region

	<u>Total count (<math>\pm</math> S.D.)</u>
Bristles	220 (39)
Supradisk	710 (229)
Oral disk	601 (115)
Chin	411 (108)
Grand Total	1942

In the data set comprising those animals for which hair counts were obtained (bristle-like hair and body hair), body weight ranged from 21-627 kg, and body length ranged from 105-329 cm. Weight and length were tightly coupled ( $r^2=0.93$  using linear regression,  $r^2=0.97$  using second order regression,  $N=14$ ), as illustrated in Figure 6. Total hair number was independent of body

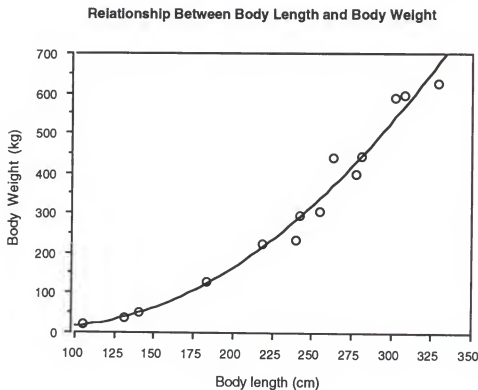


Figure 6. Body weight is tightly coupled to body length in the animals in which hair counts were made ( $r^2=0.97$ ,  $N=14$ ).

size, whether regressed against body weight ( $r^2=0.09$ ) or body length ( $r^2=0.04$ ). Total hair number was also independent of face area ( $r^2=0.0002$ ), which scales with body weight ( $r^2=0.86$ ).



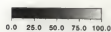
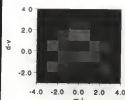
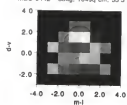
### Density of Facial Hairs

Hair (bristle-like hair and body hair) is much denser on the face than on the remainder of the body. The bristle-like hairs of the oral disk are 36% ( $\pm 19$ ) more densely packed than are the typical hairs in the supradisk region. There was no significant right-left difference in overall hair density ( $p=0.09$ ). Bristle-like hairs in the oral disk appear to be uniformly distributed, whereas hairs in the supradisk region are consistently most dense around the nares, and least dense around the caudal periphery (Figure 7).

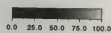
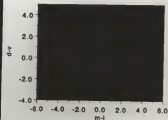
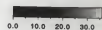
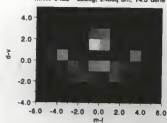
As described above, the total number of facial hairs, although variable, is independent of body size. However, as illustrated qualitatively in Figure 7, younger animals have a greater density of hair on the face than adults. Raw density values are reported as collected and therefore appear in units of hairs/ $4\text{ cm}^2$ . The combined hair density of the oral disk and supradisk regions decreases as face area increases ( $r^2=0.89$ , second order fit), in an asymptotic fashion (Figure 8). Because face area is strongly correlated with body weight ( $r^2=0.86$ ), this corresponds to a three-fold decrease in hair density with growth, from approximately 35 hairs/ $4\text{ cm}^2$  in individuals weighing less than 100 kg, to approximately 10 hairs/ $4\text{ cm}^2$  in older animals (over 300 kg or 240 cm) (Figure 9). This compares to a much lower density of approximately 0.20 hairs/ $4\text{ cm}^2$  on the remainder of the body in adults. These findings imply that a fixed number of hair follicles occupy an increasing facial area during the growth of each individual.

Figure 7. Hair distribution and density on the Florida manatee oral disk and supradisk, for a neonate (MEC 9442), a juvenile (MNW 9422), and a large adult (SWFTM 9318B). Body weight, face area, and facial hair density accompany each animal id. Hair distribution and density is plotted in  $4 \text{ cm}^2$  squares, on both auto-scaled (left column) and normalized (right column) plots. The midline corresponds to m-1 (0.0), and the boundary between the oral disk and supradisk (orofacial ridge) is at d-v (0.0). Total hair number was similar in all three cases (left column), but density decreases as body and face size increase (right column).

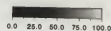
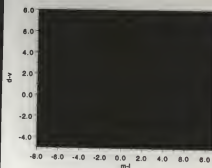
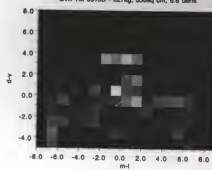
MEC 9442 - 38kg, 104sq cm, 33.3 dens



MNW 9422 - 222kg, 248sq cm, 14.3 dens



SWFTM 93188 - 627kg, 536sq cm, 6.6 dens



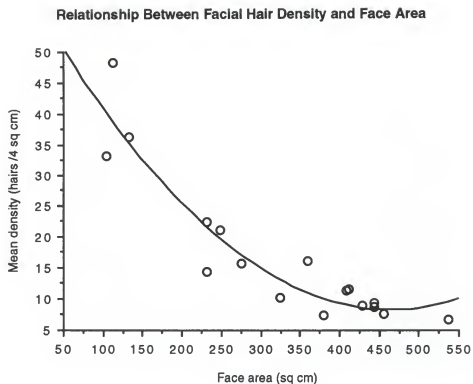


Figure 8. The combined density of hair on the supradisk and bristle-like hair on the oral disk decreases with face area. ( $r^2=0.89$ , second order curve fit;  $N=17$ ).

#### Innervation of Facial Musculature and Perioral Bristles

The nerves that innervate the perioral region were visible superficially after removal of the skin and underlying connective tissue. Superficially, the dorsal and ventral branches of the buccal branch of the facial nerve were the most visible nerves. The dorsal buccal branch courses over the masseter muscle on the lateral side of the face. When traced rostrally, the dorsal buccal nerve becomes less superficial as it dives deep to the facial muscles rostral to the *M. masseter*. At this point the nerve branches into many small terminal fibers which innervate the muscles of the upper lip and nasal area (Figure 10A),

including the *M. centralis nasi*, *M. levator nasolabialis*, *M. lateralis nasi*, *M. sphincter colli profundis pars oris*, and *M. maxillonasolabialis*, all of which have been implicated in feeding behavior (see Chapter 3).

On the lower jaw, the ventral buccal nerve is also visible superficially as it branches from the common trunk of the buccal branch of the facial nerve. The ventral buccal nerve emerges from the main trunk of the facial nerve, which exits the skull via the stylomastoid foramen. This foramen is visible just caudal to the very prominent tympanic bulla. The ventral buccal nerve courses just beneath the skin and lateral to the muscles of the lower jaw. It divides into smaller branches that then course deep to the muscles of the lower lip, where

#### Relationship Between Facial Hair Density and Body Weight

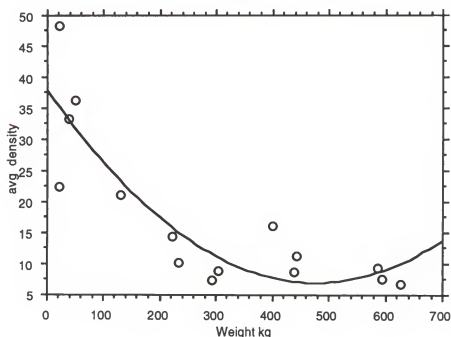


Figure 9. Density of hair and bristle-like hair decreases as body weight increases ( $r^2=0.77$ , second order fit;  $N=15$ ).

they terminate as motor nerves to the *M. mandibularis*, *M. mentalis*, and *M. orbicularis oris* muscles (Figure 10A).

Deep to the *M. levator nasolabialis*, the infraorbital branch of the maxillary nerve can be found. This sensory branch of the trigeminal system leaves the skull via the infraorbital foramen as a large bundle of several separate nerve fibers. These fibers course rostrally, deep to the branches of the dorsal buccal nerve, and separate into smaller fibers. These smaller fibers terminate on the bases of the connective tissue capsules of each facial bristle follicle in the U1-U4 fields (Figure 10B).

Finally, the sensory innervation of the lower jaw is carried by the mandibular division of the trigeminal nerve. This nerve exits the skull via the oval foramen, and can be seen entering the lower jaw caudal to the incoming molars. The nerve then courses rostrally medial to the mandible and branches into three separate trunks. The lingual branch is directed medially and provides innervation to the tongue. The mylohyoid nerve courses ventrally, and innervates the *M. mylohyoideus* as well as the skin of the ventral mandible. The inferior alveolar branch continues rostrally within the mandibular canal and exits via three mental foramina. Its terminal branches are the mental nerves, which innervate the connective tissue capsules of the individual bristle follicles in the L1 and L2 fields (Figure 10C).

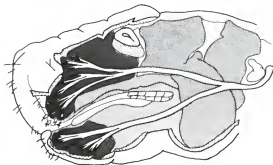
## Discussion

### Perioral Bristles

The pattern of perioral bristle distribution in manatees is unlike that of the vibrissae of any other mammalian order. This undoubtedly reflects the

Figure 10. Left lateral cutaway views of postmortem heads of *Trichechus manatus latirostris*. In **A** the course of the dorsal and ventral buccal branches of the facial nerve are indicated. They terminate in muscles of the face and lower jaw, respectively. Panel **B** illustrates the course of the infraorbital branch of the trigeminal nerve, which exits the skull via the infraorbital foramen and terminates near the bases of individual facial bristle and hair follicles. In panel **C** the inferior alveolar branch of the mandibular division of the trigeminal nerve courses in the mandibular canal and exits via the mental foramina to terminate on individual bristle and hairs follicles.

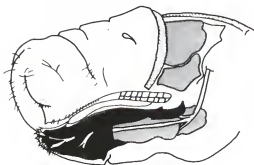
A. Facial nerve - dorsal and ventral buccal branches



B. Trigeminal nerve - infraorbital branch



C. Trigeminal nerve - inferior alveolar branch





specialized anatomy of the entire perioral region in manatees, whereby the lips (and hence, some of the bristles) lie partly inside the oral cavity. The unusual appearance of manatee bristles compared to vibrissae in other mammals, and the prehensile use of the bristles by manatees, were noted by early investigators (Vrolik, 1852; Chapman, 1875; Garrod, 1879; Murie, 1880).

Other aquatic mammals exhibit very different vibrissae patterns. In cetaceans, vibrissae are greatly reduced or absent, some are present only in fetal stages (Ling, 1977). In contrast, members of the Order Pinnipedia possess many long mystacial vibrissae which are actively swept in a coordinated fashion during displays and tactile exploration (Stephens *et al.*, 1973; Ling, 1966; Peterson and Bartholomew, 1967; Miller, 1975; Kastelein and van Gaalen, 1988; Kastelein *et al.* 1990). In a comparative anatomical survey of thirteen mammalian orders including terrestrial and aquatic taxa, Pocock (1914) defined five vibrissae fields and described taxonomic variations in their distributions and relative densities. Huber (1930a, 1930b) emphasized the constant relationship between each vibrissae field and specific superficial facial muscles and the innervation across mammalian taxa. Mystacial vibrissae are innervated by the infraorbital nerve. Innervation of the manatee upper bristles by branches of the infraorbital nerve was first noted by Murie (1872). Mental vibrissae are innervated by the mental nerves (Huber, 1930a, 1930b), consistent with findings for the lower bristles of the manatee. These relationships, together with bristle-muscle associations (see Chapter 4) suggest that the U1-U4 bristles are homologous to the mystacial vibrissae of other taxa, and that the L1 and L2 bristles correspond to the mental vibrissae.

The present findings suggest an intriguing face-brain relationship. Rindenkerne are clusters of neurons in layer VI of certain areas of sirenian

cerebral cortex, and they are most prominent in the presumptive face area of somatic sensory cortex (Reep *et al.*, 1989; Loerzel and Reep, 1991; Marshall and Reep, 1995a). I have hypothesized that each manatee bristle is represented by a single large Rinden Kern, as is the case for rodent vibrissae and cortical barrels in layer IV of somatic sensory cortex (Simons 1978). The 110 perioral bristles per side of the manatee face are matched by a similar number (116) of large (>350 mm diameter, >300 mm length) Rindenkerne (unpublished observations). It is also possible that each body hair is represented by one of the smaller Rinden Kern. However, there appear to be approximately twice as many hairs as small Rindenkerne, and some of these Rindenkerne are in areas not thought to be part of somatic sensory cortex (Marshall and Reep, 1995a).

### Facial Hairs

In the oral disk and supradisk regions of the face, total hair number is independent of body size and face area. However, hair density was inversely related to these parameters, suggesting that a constant number of follicles occupies an ever increasing area as growth proceeds. This conclusion is consistent with the findings of Szabó (1958), who counted follicles in specific regions of human fetuses, then estimated adult densities based on known growth rates of those regions, and assuming constant follicle number. The predicted densities closely matched measured adult densities, providing evidence that a fixed number of hair follicles is generated in early development, and follicles are not formed *de novo* in adults. Although individual follicles normally undergo cycles of activity and quiescence, newly developing follicles have not been reported in adult skin, except in the cases of

deer antler velvet and wound healing (Billingham, 1958). In the latter instance, intact dermal papillae are required for follicle regeneration.

### Architecture of the Face

Naturally occurring landmarks of the face, such as the orofacial ridge and the postnasal crease, are correlated with differences in the organization of the epidermis, sub-dermal connective tissue and adipose tissue. The oral disk is a supple, softer region when observed in live animals. The supradisk is a firmer, less supple region. These differences are still noticeable well after death. Upon dissection, the oral disk region is depauperate in subdermal fat and connective tissue and the epidermis is thin, whereas upon dissection, the supradisk region consists of thick epidermis and greater amounts of subcutaneous fat and connective tissue. These differences in anatomy are correlated with the different functional roles of the two regions during feeding and other tactile activities. Such architecture is seen in other organisms in which muscular hydrostats (Kier and Smith, 1985) are important in feeding and locomotion. Muscular hydrostats will be described in further detail in relation to manatees in Chapter 4.

CHAPTER 3  
PREHENSILE USE OF PERIORAL BRISTLES DURING FEEDING AND  
ASSOCIATED BEHAVIORS OF THE FLORIDA MANATEE (*Trichechus manatus*  
*latirostris*)

Introduction

Manatees possess a short muscular snout which is covered by short sinus hairs and modified vibrissae, or perioral bristles (Chapter 2). These modified vibrissae are short, thick, and robust compared to the mystacial vibrissae of terrestrial mammals and are found in the perioral region. Florida manatees use this vibrissal-muscular complex in a prehensile, grasping manner to bring vegetation into the oral cavity and to manipulate inanimate objects in their environment. These observations were first mentioned by Chapman (1875). He described feeding manatees as "fanning" food into their mouths using "bristles situated on their upper and lower lips." Later, Garrod (1879) described the feeding behavior of a captive manatee in greater detail. He referred to the bristle fields as pads and stated that when an animal is about to grab a piece of vegetation, ". . . the pads are diverged transversely in such a way as to make the median gap of considerable breadth." The two lip 'pads' are approximated, grasping the food and drawing it into the mouth by a ". . . backward movement of the lower margin of the lip . . ." Garrod (1879) described the feeding behavior as being similar to that of a caterpillar feeding upon a leaf. Murie (1880) described the action of perioral bristles as ". . . seize[-ing] [food] with its bristle-clad lips . . ." and having ". . . great mobility and special use of the inner circumscribed bristle-clad portions of the upper lip." Allsopp (1961) compared

the feeding behavior to that of ungulates and as moving in a sideways fashion. Ling (1977) simply mentioned that manatee vibrissae are "very mobile." Hartman (1979, p. 85) stated that the lips are bi-lobed and covered with bristles and described the action of feeding. "The lobes are everted, projecting the bristles into the food source, then closed laterally, forcing the bristles to grasp the vegetation, tuck it in the cleft between the lobes and funnel it to the mouth."

The use of vibrissae by manatees to manipulate food and objects in their environment is a departure from the classical function of mammalian vibrissae. Other mammals use vibrissae to detect tactile cues; many pinnipeds employ "whisking" movements for more directed tactile exploration. For example, California sea lions (*Zalophus californianus*) possess extremely mobile vibrissae which can be rotated from the resting position along the side of head to extending almost directly forward from the muzzle (Peterson and Bartholomew, 1967). The sniffing behavior and related vibrissal movements of the albino rat during exploration have been examined in great detail. These behaviors involve sweeping of the mystacial vibrissae forward and backwards in conjunction with protraction and retraction of the rhinarium and head (Welker, 1964). The modification of manatee perioral vibrissae (bristles) for manipulation of food and other objects in a prehensile manner appears to be unique to sirenians. Previous descriptions of the function of the perioral bristles of Florida manatees are brief and lack detail. My objective was to explore the range of behaviors involving the vibrissal-muscular complex of Florida manatees, and to determine the importance of bristle use to the feeding ecology and sensory perception of this species.

### Methods

The range of behavioral plasticity of the muscular snout and perioral bristles of Florida manatees was elucidated using several methods and study sites. Captive manatees were presented with several types of vegetation and inanimate objects. Wild manatees were observed at the Crystal River Refuge (CRR), Crystal River, FL and in the blue headwaters of the Homosassa River (HR), Homosassa, FL. At these study sites, individuals were observed feeding upon aquatic vegetation and interacting with inanimate objects as well as with conspecifics.

Feeding trials were conducted at three facilities where manatees are kept in captivity: Homosassa Springs State Park (HSP), Homosassa, FL; Lowry Park Zoological Gardens (LPZ), Tampa, FL; and Sea World of Florida (SWF), Orlando, FL. A total of seventeen animals, five females and twelve males, were used in this study. Four species of freshwater vegetation, *Hydrilla verticillata* (Hydrilla), *Myriophyllum spicatum* (Eurasian water-milfoil), *Vallisneria americana* (tapegrass or wild celery), and *Eichhornia crassipes* (water hyacinth), and two species of seagrass, *Syringodium filiforme* (manatee grass) and *Thalassia testudinum* (turtle grass), were used for feeding trials. All plant species used in this study are normally consumed by free ranging Florida manatees.

Feeding trials employed a piece of plexiglass (80 cm x 90 cm) into which 1 cm diameter holes were drilled at 10 cm intervals (Figure 11). Prior to each feeding trial, stems of vegetation were pushed into the holes of the plexiglass. Only one species of aquatic vegetation was presented during any single trial. An underwater viewing window was used at LPZ for the duration of the study and at HSP for the first field season. Suction cups were fixed to each corner of the plexiglass, which was then affixed to the underwater viewing window. By

placing the plexiglass on the window in this manner, I obtained a close-up view of the perioral region through the plexiglass while the animals fed.

Manatees at LPZ (three males) and HSP (three females) were fed each of the six species of vegetation between the months of May and August during two years (1993 and 1994). The 1994 summer trials represent a statistically balanced research plan, whereby each species of plant was presented to each manatee at LPZ and HSP once a week for a total of ten weeks. Manatees at SWF (five males) were also presented with the same species of plants within a statistically balanced research plan for total of five weeks during the summer months (1995). The total number of 514 feeding trials were conducted.

I attempted to control the order in which plant species were presented to specific individuals. An ordered sequence of feeding trial presentations helps to ensure that any vegetation type has an equal chance of being in any presentation to a given manatee. The daily sequence in which each plant species was presented was changed for each session. Logistically this often proved to be difficult. Under certain circumstances, feeding trials were conducted opportunistically; my desire to present a certain type of aquatic plant to a particular individual was often compromised by manatee behavior. For example, during the feeding trials, I attempted to present a specific species of plant to a specific individual. Often this individual would wander away and a different individual would approach the plexiglass and try to eat the plants. If the second individual was not recorded feeding on that plant species for that day, I would allow the second individual to feed. When attempting to present a specific plant to a specific individual, often that individual would decide not to eat this type of vegetation. A second piece of plexiglass filled with a different

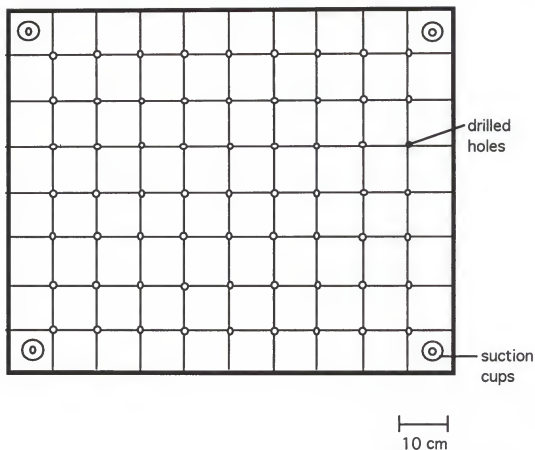


Figure 11. Rectangular plexiglass which is use to present vegetation to manatees. Plants are pushed into the holes, which are approximately 10 cm apart.

species of vegetation was often ready and would be switched with the first piece of plexiglass. Most of the time the individual would eat the vegetation from the second plexiglass. The first plexiglass with the original vegetation would then be replaced and the same individual would immediately consume the desired vegetation.

Feeding trials were conducted between the hours of 0900 and 1500, although most trials were completed by 1300 hours. At LPZ, morning feeding schedules conducted by zoo-keepers were delayed until after the feeding trials were completed. This insured motivation to feed. Normal feeding regimens



were not altered at HSP and SWF; feeding trials were conducted around these times.

Manatees in the study quickly learned that feeding trials involved novel food items. Usually, manatees appeared to prefer freshly collected vegetation to their normal diet (Romaine lettuce, cabbage, carrots, etc.). Satiation of individuals did not appear to be a problem. Individual preferences were qualitatively observed to occur. Occasionally, an individual would be reluctant to eat certain types of vegetation; during these trials the animals explored the plexiglass, mouthing the vegetation with its lips and bristles but would not eat. Once a different type of vegetation was presented that same individual would always consume the plants. I interpret this type of behavior as individual preference. Preference varied among individuals and appeared to change from day to day. In order to ensure that typical feeding behavior was recorded, only feeding trials in which manatees ate approximately 80 to 90% of the vegetation presented were used for data analysis and calculation of mean feeding rates.

Behavior was recorded using a Yashica model KD-H170u Hi8 format video camera and evaporated Hi8 videotape. All Hi8 video tapes were backed up using S-VHS videotape. Feeding trials at HSP and SWF differed slightly in methodology from those at LPZ. At the former sites, using the underwater viewing windows was impractical. Instead, a mobile underwater viewing window was constructed from PVC tubing, in the shape of a cube in which the Hi8 video camera (in an Amphibico underwater housing) was positioned (Figure 12). The underwater video camera faced one side of the cube which was covered with a removable piece of plexiglass. Holes were drilled into this piece of plexiglass and vegetation was placed in the plexiglass as described above. Styrofoam floats were attached to the top of the PVC cube, enabling the underwater window to float just below the water's surface. This apparatus proved to be invaluable in

helping to isolate and present vegetation to a single animal in the presence of many other hungry manatees. In addition, manatees were videotaped feeding upon free-floating water hyacinth using the underwater video camera alone to determine if differences existed between feeding upon floating vegetation versus submerged vegetation.

During the summer months of 1995 (May through August), inanimate objects were presented to captive manatees at LPZ. Manipulation of non-food objects by manatees was videotaped in order to better understand the range of manipulative behavior involving perioral bristles. Several items were placed in the manatee holding tank. Two identical sets of acrylic polygons of seven different shapes (triangle, circle, square, rectangle, pentagon, star, and modified square) were attached to two separate sheets of plexiglass (Figure 13). Polygons were constructed of 1.25 cm (1/2 inch) thick acrylic with approximate

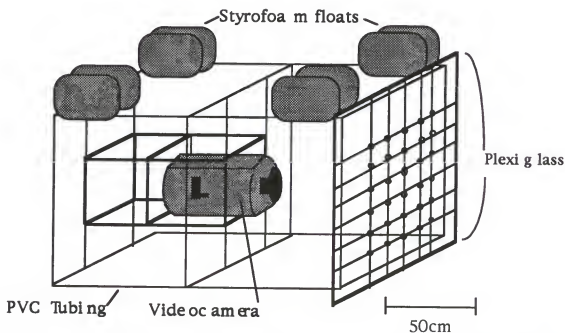


Figure 12. Mobile underwater window. This apparatus consists of a PVC frame (cube) in which a removable piece of plexiglass is attached at one end. An underwater video camera and housing is positioned to record the perioral region of feeding manatees. The top of the structure floated just below the surface of the water.

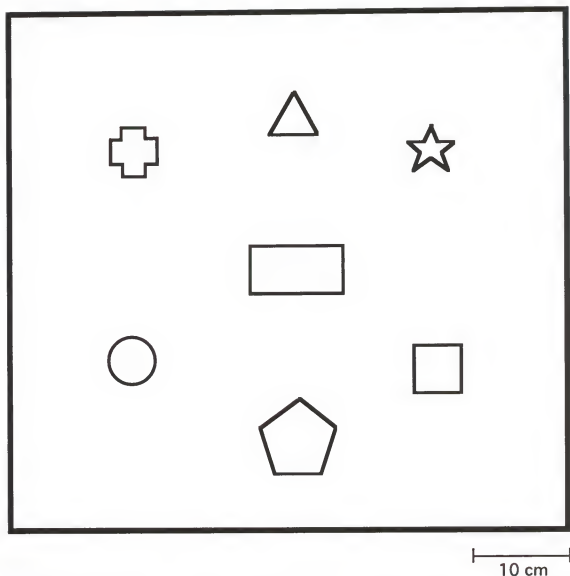


Figure 13. Schematic diagram of plexiglass with of acrylic polygons presented to manatees.

dimensions of 15.5 cm (5 inches) in height and width. One set of polygons had roughened surfaces and one set had smooth surfaces. Each polygon was affixed to the plexiglass sheet with acrylic cement. In addition, a hole was drilled through each polygon and the sheet of plexiglass, and a brass nut and bolt were fastened to provide additional strength. Both polygon sets were placed on different underwater windows in the same manner as in the feeding trials. A floating square frame also made of PVC and styrofoam floats was anchored in

the center of the tank. This apparatus contained two lengths of rope per side (two ropes, 2.5 cm (1 inch) in diameter and made of cotton fiber; two ropes 2.5 cm (1 inch) in diameter and made of nylon fiber; two ropes 1.25 cm (1/2 inch) in diameter and made of nylon fiber with a diamond braid; two ropes 0.63 cm (1/4 inch) in diameter and made of nylon fiber, weave braid) for a total of eight ropes presented. These were dangled in the water column (Figure 14). A single figure eight knot was tied at the end of each rope.

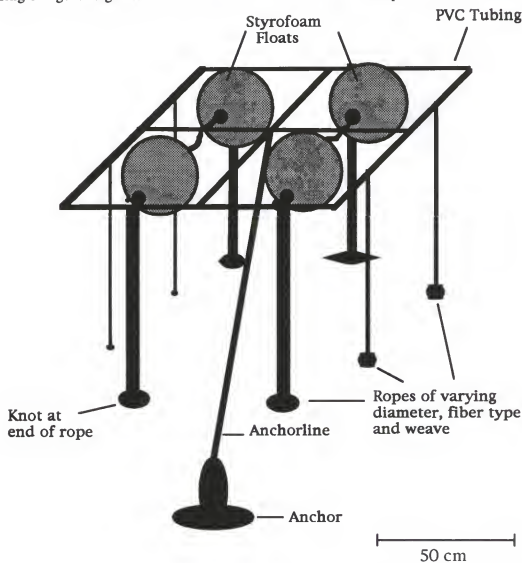


Figure 14. Schematic diagram of PVC apparatus to present ropes of varying diameter and fiber type to manatees.

Videotapes of manatee behavior were analyzed in real time, slow motion, and frame by frame to determine the component movements of the bristles, snout and associated structures. Analysis of videotape was performed on a Panasonic model AG-7300 S-VHS editor in conjunction with either an IBAS computer imaging system (Kontron Image Analysis Division) which supported a black and white imaging monitor, or a Sony Trinitron model PVM-1350 color video monitor.

## Results

### Submerged Vegetation

Manatee feeding involves rhythmic movements of the lips, perioral bristles and jaws. Designations of the bristle fields are as defined in Chapter 2. The most common sequence of movements observed when manatees ingest submerged vegetation is as follows (Figure 15):

- A. The most rostral muscular portion of the snout contracts in the rostro-caudal direction. This action pulls the oral disk dorsally and exposes the U2 bristles to the vegetation.
- B. The U2 bristles evert forward then are moved medially to bring the plant material toward the midline of the body in a lateral to medial sweeping motion. The lower jaw begins to open at this time.
- C. The right and left U2 bristles reach apposition at the midline and push vegetation into the oral cavity; the lower jaw is now maximally open. The L1 bristles evert from their fleshy pad.
- D. The U2 bristles diverge laterally and the lower jaw begins to close.
- E. As the lower jaw closes, the L1 bristles sweep vegetation further caudally into the mouth. The U2 bristles arrive at their original and lateral position. A new grasping cycle then begins.

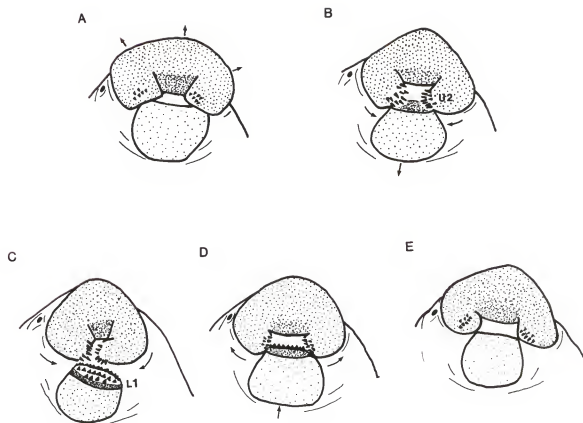


Figure 15. Schematic diagrams from five representative videotape frames of a manatee feeding upon submerged vegetation positioned in the plexiglass. Arrows indicate direction of movements of the "flare" behavior (A), U2 bristle fields (B, C, and D), and lower jaw (B and D). See text for details.

I define each sequence of events as a single feeding cycle. Each cycle has a mean duration of 610 ms (S.D.=52.9, N=17). Together, the right and left U2 bristle fields are involved as a prehensile apparatus during feeding. The L1 bristle field actively pushes vegetation further into the oral cavity upon closure of the lower jaw. The U2 and L1 bristle field actions alternate with each other, resulting in the continual movement of vegetation into the oral cavity. The U1 bristle fields are naturally everted throughout the cycle, but play no active role in food gathering. They may be involved in tactile exploration during feeding. The remaining bristle fields (U3, U4, L2) are difficult to visualize on the video because of their more caudal locations in the oral cavity. However, I made direct visual observations of these fields when in close proximity to animals. The U3, U4, and L2 bristle fields which appear to passively aid in the movement of food further into the oral cavity. For example, as the U2 fields reach out to grasp vegetation, the lateral margins of the upper bristle pad (which contain the U3 and U4 bristle fields) are raised and moved forward. As the U2 bristles introduce vegetation into the mouth, the bristle pad margins are lowered and moved in a caudal direction. Therefore, the U3 and U4 bristles are moved in a circular fashion; this motion directs food further into the mouth in a passive manner relative to the action of the U2 bristle fields. Similarly, the L2 bristle fields move vegetation passively into the oral cavity, in conjunction with the more active movements of the L1 bristle field.

### Floating Vegetation

The grasping pattern of the feeding cycle often differs when manatees are feeding upon floating vegetation such as *Eichhornia crassipes* (water hyacinth). Then, the U2 bristle fields have been observed acting individually

or together (right and left sides) in a raking fashion. The upper lip(s) reach out for the vegetation with the upper bristles extended and pointed downward, and attempts to drag it closer to the mouth. Multiple reaching motions are usually required to accomplish this act. When the plant is firmly held by the bristles, individuals almost always grasp the plant with both flippers and sink below the surface to feed. The usual cyclic grasping movements seen when manipulating submerged vegetation (described above) are then employed to pass the vegetation into the oral cavity.

### Other Manipulative Behaviors

Other manipulative behaviors involving the perioral vibrissal-muscular complex were observed. The left and right U2 bristle fields can act independently under certain conditions. During feeding upon submerged vegetation, both U2 bristle fields are normally brought together symmetrically at the midline in a lateral to medial sweeping motion. The orientation and medial extension of each U2 bristle field appears equivalent during this event. However, when grasping food that is difficult to free from the plexiglass, manatees often used only one U2 bristle field or both right and left U2 bristle fields, but in a non-prehensile manner, such as when dragging the vegetation from the hole. Another variation was the use of both U2 bristle fields in a prehensile manner in which the bristle fields did not meet at the midline, but overlapped in order to free the object of interest. For example, a portion of a whole carrot was wedged between the plexiglass and the underwater viewing window at LPZ. One individual spent approximately two minutes tugging and pulling on the end of the carrot until it was freed from behind the plexiglass (Figure 16C). During this manipulation of the carrot, this particular individual



displayed a wide range of precise, coordinated movements and prehensile abilities not previously documented. In such cases the orientation and medial extension of each U2 bristle field were markedly unequal. In addition to this strategy, the L1 bristle field is often used alone to scrape vegetation off the plexiglass as the animal moves from the bottom of the plexiglass to the top.

Manatees were observed to reverse the direction of the U2 bristle fields either together or independently. This often occurs when an individual appears to dislike the taste or texture of the vegetation or part of the vegetation ingested. Several individuals were observed to reverse the direction of one U2 bristle field from a lateral-to-medial direction to a medial-to-lateral direction while the other U2 bristle field maintained the original direction (lateral to medial). During these events, individuals are able to extract the undesirable food item from one side of the oral cavity (Figure 16A). This suggests that manatees possess a high level of perioral tactile discrimination and dexterity.

Often the perioral bristles and associated bristle-like hairs (Chapter 2) appear to be used in a tactile, exploratory fashion. As vegetation is consumed during the feeding trials, individuals begin exploring the remainder of the plexiglass for additional vegetation. This behavior involves quick side-to-side movements of the snout region in a quivering motion while the animal sweeps the entire head side to side as well as up and down. When a piece of vegetation is encountered, the individual may use both U2 bristle fields to grasp the vegetation from the side, position the mouth over the piece of vegetation, or attempt to drag the vegetation toward the mouth with one or both U2 fields or the L1 fields.

It is of interest that the eyes are often closed during feeding and exploratory behavior. Closing of the eyelids would protect the eyes when feeding upon a silty substrate or among plant stalks. In addition, shutting down

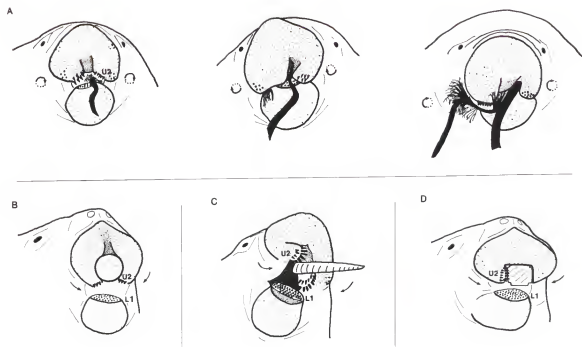


Figure 16. Schematic diagrams from videotape frames of non-food manipulative behavior. Arrows indicate direction of U2 bristle fields. A. Reversal behavior of U2 bristle direction. B. Non-perioral bristles, muscular grasping behavior. C. Independent use of left and right U2 bristle fields. D. Use of U2 bristles during exploration of a novel object. See text for details.

one sensory system (vision) that has limited value in a particular situation may enhance other sensory modalities such as touch. The oral disk and its bristle-like hairs are sensitive to human touch; if one touches any portion of the oral disk, the U2 bristles grasp for the stimulus. Pectoral flipper use was greatest when feeding upon floating vegetation. However, flippers were used occasionally to pull or push off the plexiglass during feeding trials. In fact, the original design of the plexiglass feeding apparatus enabled some manatees to place their flipper behind it and pull it off the window. Once individuals learned that the plexiglass could be removed, this behavior was repeated again and again until I changed the method of anchoring the suction cups to allow the plexiglass to be positioned closer to the window (a change in distance of approximately 2 centimeters).

### Inanimate Objects

Manatees "chew" on non-food objects naturally in the wild (Hartman, 1979; Beck and Barros, 1991) as well as in captivity (personal observation). Three manatees at LPZ were presented with objects designed to aid in the understanding of the range of perioral manipulative behavior. Two sets of acrylic polygons (smooth and roughened) and several ropes of varying fiber types and diameters were placed in the holding tanks. Manatees did not seem to prefer any set of inanimate objects over another. Animals explored the plexiglass, presumably for vegetation (or out of curiosity). Once the plexiglass was discovered to contain no vegetation, the individual usually moved on. During directed exploration of polygons, the U2 bristle fields moved back and forth over the edges of the polygons and the head was moved side to side in a sweeping manner (Figure 16D). During such behavior, manatees also seemed to

brush the objects with the bristle-like hairs which are distributed over the oral disk (Chapter 2). Such behavior also occurred when hand-feeding monkey biscuits (used to supplement the diet and as a vehicle to administer multi-vitamins) to manatees. Individuals approached the hand, touched the biscuit with the hair on the oral disk (occasionally moving their head back and forth and up and down if necessary) and then grasped the biscuit with the U2 bristles. Occasionally, an individual grasped a polygon with the entire vibrissal-muscular complex, wrapping the muscular lips and perioral bristles around the perimeter, tightening its grip and attempting to remove the polygon from the plexiglass (Figure 16B).

Manipulation of ropes by manatees was observed in the wild and in captivity. During one occasion while observing wild manatees at CRR using a mask and snorkel, I was followed by a small calf for 30 minutes, during which time it grasped for and chewed at the rope attached to a dive flag which trailed from my ankle. It is not uncommon for manatees to spend 20 to 30 minutes "chewing" or manipulating anchor lines at CRR. Two types of behaviors were noted in wild and captive animals: individuals brought parts of the rope into the mouth and used their muscular lips and bristles to manipulate knotted portions of it. Both the U2 bristles and the L1 fields were used in the same manner as when feeding on submerged aquatic vegetation. On one occasion, a wild individual took an anchor line into its mouth, then gently touched, explored and manipulated the rope as it moved down along the length of the rope. When the individual encountered a knotted loop of rope, it spent approximately 10 to 20 minutes moving the knotted loop around inside the mouth using the U2 and L1 perioral bristles. In other instances, individuals brought the rope into the mouth perpendicular to the long axis of the body, pushed the rope to the

corners of the mouth using the U2 and L1 bristle fields, and presumably chewed the rope with the teeth.

### Comparisons with other taxa

Several pinnipeds including the harbor seal (*Phoca vitulina*), ringed seal (*Phoca hispida*), southern elephant seal (*Mirounga leonina*), California sea lion (*Zalophus californianus*), Steller's sea lion (*Eumetopias jubatus*) northern fur seal (*Callorhinus ursinus*), and walrus (*Odobenus rosmarus divergens*) were observed in captivity to determine if vibrissal use was prehensile in nature. On several occasions, trainers placed objects and/or food near the animals' vibrissae to test for prehensile ability. All pinnipeds observed possessed "whisking" ability, but no prehensile behavior was seen. Of the pinnipeds observed, the orofacial anatomy of the walrus most closely resembles that of the manatee. Six walruses from SWF and Futami Sea Paradise Aquarium, Futami City, Mie Prefecture, Japan, were observed. The action of walrus vibrissae is manipulative; walruses are able to use the vibrissae to move food toward the mouth. This is accomplished by passing food particles from vibrissa to vibrissa in a wave-like manner until the food either falls into the mouth, is grasped by the muscular lips (but not vibrissae), or brought close enough to the mouth to allow the animal to use its suction ability to feed. At no time were walruses observed to grasp the food particles with their vibrissae.

### Discussion

The manatee's role as an obligate aquatic herbivore requires certain adaptations to survive in this niche. Aquatic vegetation is an ubiquitous but

low-quality food source. Manatees may spend 5 to 8 hours a day feeding and consume approximately 10% of their body weight per day (Hartman, 1979; Bengtson, 1983; Etheridge *et al.*, 1985). Florida manatees are able to feed at any position in the water column (Hartman 1979, Domning 1980). However, because much of the vegetation encountered is submerged, submerged feeding behavior is considered more common than surface feeding in the wild. The mean manatee feeding cycle length I observed for animals feeding upon submerged vegetation is best compared with feeding trials conducted by Bengtson (1983) and Etheridge *et al.* (1985). Both of these studies used hydrophones to record chewing rates of manatees. The present mean feeding cycle mean of 610 ms (1.64 chews per second) falls between chewing rate values reported by Bengtson (1983)(1.05 chews per second) and Etheridge *et al.* (1985)(1.86 chews per second). Since introduction of food into the mouth is likely to be intimately linked with mastication it is likely that feeding cycle length is inversely related to chewing rate, and these are two different measurements of feeding.

Hartman (1979) described several interactions (sexual and non-sexual) between conspecifics that involved perioral bristles. Sexual and non-sexual behaviors are often difficult to distinguish. Most interactions include mouthing, nuzzling, nudging, and embracing (Hartman, 1979). Of these behaviors reported by Hartman, I have observed that mouthing and nuzzling involve perioral bristles. Mouthing predominantly involves the U2 bristle fields but also occasionally the L1 bristle fields. I agree with Hartman (1979) that mouthing and nuzzling behaviors are social in nature. Manatees occasionally would push and shove at each other in order to position themselves to feed upon the vegetation. During these events some individuals used the U2 bristles to pinch the back, flipper or tail of a conspecific. On a number of occasions, an assistant was pinched in tender areas by the U2 bristles and can

attest to the force used and discomfort incurred. On other occasions, mouthing behavior appeared to be play behavior (Hartman, 1979) instead of a dominance behavior. Often individuals in captivity and in the wild were observed to explore the back of a conspecific, gently caressing or scratching the dorsum and often picking off algae or loose skin. The action of the robust bristle fields (U2 and L1) was similar to that observed during feeding on submerged vegetation. However, the degree to which they were used varied. Nuzzling is defined by Hartman (1979) as ". . . minor variations of mouthing." Muzzle-to-muzzle contact, often termed "kissing behavior", was observed occasionally. During such contacts, only the tactile bristle-like hairs on the oral disk are usually used; the U2 and L1 bristles appeared to have little to no function during this behavior.

It has been demonstrated that evolution of supernumerary teeth (as well as other adaptations) is a result of selection pressures aimed at a particular kind of aquatic herbivory (Domning, 1982). Selection pressure to maximize ingestion of aquatic plants is apt to have been high throughout the evolutionary history of sirenians. It is reasonable to assume that natural selection was not acting on tooth morphology (or rostrum deflection) and mechanics alone, but upon the entire feeding apparatus, including soft tissue structures such as the perioral bristles and surrounding musculature. The functional significance of the manatee feeding apparatus may be that it allows the manatee to exploit many types of habitats as a generalist herbivore. The vibrissal-muscular complex and associated behavior are likely an adaptation that allows manatees to maximize the efficiency of grazing and browsing on large quantities of a variety of aquatic vegetation.

Tactile information is an important cue to most mammals. However, certain mammals possess or exhibit elaborate vibrissal form, density and even

function. Pinnipeds are a group known for their well-developed vibrissae (Peterson and Bartholomew, 1967; Ling, 1977; Fay, 1982; Hyvärinen, 1989). Most notably, the walrus and bearded seal have very dense arrays of elongated vibrissae (Burns, 1981; Fay, 1982; Kastelein and van Gaalen, 1988; Kastelein *et al.*, 1990; Reidman, 1990). I contend that sirenians are the only mammals known to use vibrissae in a prehensile manner.

The complexity and nuances of manatee behavior involving the vibrissal-muscular complex attest to the tactile nature of these animals. Manatees are often found in shallow turbid waters; in such systems, acquisition of vegetation by vision alone is not efficient. In addition to the perioral bristles, manatees also possess short sinus hairs (bristle-like hairs) in the perioral region which are sensitive to tactile stimulation (Chapter 2). It is likely that manatees rely heavily upon tactile cues to detect aquatic vegetation and perhaps even use tactile hairs to distinguish types of vegetation. Considering the habitats Florida manatees frequent and their tactile nature, is it reasonable to assume that manatees have developed complex sensory systems to detect tactile cues (Watkins and Wartzok, 1985). Neuroanatomical data support this expectation. Manatees possess well developed trigeminal-related somatic sensory nuclei (Johnson *et al.*, 1986, 1987) and neural aggregations in somatosensory cortex which are speculated to be related to processing sensory information from vibrissae (Reep *et al.*, 1989; Marshall and Reep, 1995a).



CHAPTER 4  
THE MUSCULAR HYDROSTAT OF THE FLORIDA MANATEE (*Trichechus manatus  
latirostris*) AND ITS ROLE IN THE USE OF PERIORAL BRISTLES

Introduction

The snout and associated facial structures of sirenians are unique to their order and reflect an adaptation to aquatic herbivory. The prehensile use of modified vibrissae and fine motor control of facial musculature allows manatees to process large quantities of aquatic vegetation efficiently (Chapters 2 and 3). Although anatomical studies of sirenians have included facial muscles (Murie, 1872; Saban, 1975; Domning, 1977, 1978; Gambaran and Souchanov, 1986), little attention has been given to an analysis of the muscular basis for movement of the perioral bristles. Surprisingly, comparative functional studies of facial musculature in mammals are few. Huber's (1930a, 1930b) review of the evolution of mammalian facial musculature revealed diverse anatomical specializations and associated variations in behavior for fish, amphibians, reptiles and birds, but focused on mammals. This comprehensive work laid the groundwork for future systematic investigations. Welker (1964) examined in detail the sniffing behavior and coordinated movements in the vibrissae of the albino rat. Compton (1973) investigated the facial musculature and associated behavior of the coati (*Nasua nasua*) which possess a specialized proboscis which is used to "touch, push, probe, fixate, overturn and move stimulus objects." Many mammalian taxa possess elaborate vibrissae in association with facial musculature and complex behavior (Huber 1930a, 1930b; Welker 1964, Compton 1973). Many mammals, including rodents and pinnipeds, appear to utilize

vibrissae in a "whisking" movement for directed exploration or display (Miller, 1975). However, the use of modified perioral bristles in conjunction with the surrounding musculature to grasp and manipulate food and other objects appears to be unique to the sirenians. The movement of the feeding apparatus of the Florida manatee has been demonstrated to be capable of complex movements (Chapter 3). These abilities are similar to the complex movements of an elephant trunk (see Murie, 1880). Elephant trunks are characterized by a lack of skeletal attachments and an increase in muscle insertions on soft tissue. In addition, the trunk muscles are organized into radial, longitudinal, transverse and circular complexes. Such structures are known as "muscular hydrostats" (Kier and Smith, 1985). These functional structures should not be confused with the term "hydrostasis" which involves immersion of objects in water to determine density or the maintenance of static equilibrium in water (Domning and DeBuffrenil, 1991). Muscular hydrostats are characterized as three dimensional arrays of muscles of constant volume, with a capability to move in highly controlled, detailed and varied movements.

In the present report, my objectives are to (1) demonstrate that the function and organization of muscles of the manatee snout are consistent with other biological structures known to be muscular hydrostats and (2) propose a functional model of the underlying muscular mechanisms for behavior involving the perioral bristles and oro-facial region (Chapter 2) in the Florida manatee.

### Methods

Six manatee heads were obtained from the State of Florida carcass salvage program. Fresh heads were frozen and then sliced into 1-2 cm thick coronal,

sagittal or horizontal sections with a band saw in a manner similar to that described by Kastelein *et al.* (1991a) for walrus. This method worked well in manatees where the rostrum is comprised of many oro-facial muscles in which muscle fibers intermingle in a complex manner. These gross sections were then stained with a modified Harris' hematoxylin and eosin stain to highlight muscle fibers and their orientation. Facial myology was then documented photographically (Figure 17). Frozen gross slices were overlain with acetate sheets, and the muscle beds and structures were outlined to create schematic drawings of the locations of facial muscles (Figure 18). Several fresh postmortem heads were used for gross dissection of the facial musculature to supplement and corroborate data obtained from sectioned heads. The lateral surface of the face and snout was dissected, from a point 3 cm caudal to the angle of the mouth, to the rostral surface of the snout cranially. The skin was removed, and underlying muscles were separated along fascial planes to determine the origins, insertions and the orientations of the muscle fibers. Superficial muscles were transected and reflected as they were isolated in order to access deeper structures. Videotape and still photographs that had been taken for another study (Chapter 3) were analyzed to correlate feeding behavior with facial musculature.

## Results

The location and nomenclature of the facial muscles are consistent with those of the Amazonian manatee as reported by Domning (1978). Eight facial muscles comprise the oro-facial region. My examination of the most rostral extent of the manatee snout has revealed an additional muscle which I have named *M. centralis nasi*. In addition, I have found that the *M. buccinatorius* in

Florida manatees has a rostral extension that is a departure from the typical mammalian arrangement (Huber, 1930a, 1930b).

The following are descriptions of our observations of Florida manatee facial musculature:

*M. Centralis nasi* (Figure 18, A-D)

Originates diffusely in the connective tissue of the mid-sagittal portion of the snout. The fibers in the caudal portion run transversely and attach to the premaxillary symphysis, ventral to the narial passages. In the rostral portion of the muscle, the fibers fan out laterally and insert on the skin of the snout.

*M. Levator nasolabialis* (Figure 18, B-F)

A fan shaped muscle that has a tendinous origin along the anterior edge of the orbit. The fibers course cranially to insert on the dorsal skin of the snout. Rostrally the dorso-lateral portion of the *M. levator nasolabialis* interdigitates with fibers from the *M. centralis nasi*. Caudal to the *M. centralis nasi* the fibers of the *M. sphincter colli profundus pars oris* (SCPO) decussate and intermingle with fibers of the *M. levator nasolabialis* and are difficult to differentiate on cross section. The approximate point of differentiation of the *M. levator nasolabialis* and the *M. SCPO* is indicated in figure 2C by a black arrow.

*M. Lateralis nasi* (Figure 18, D-F)

Originates on the dorso-lateral surface of the premaxilla. The fibers project laterally in a mass through which runs a neurovascular bundle including the dorsal buccal branch of the facial nerve. The majority of the fibers terminate on the fascial surface of the *M. maxillonasolabialis*, but some of the fibers continue into its belly. On the ventral and caudal origin of the *M. lateralis nasi*, the fibers are indistinguishable from those of the *M. buccinatorius*. A slip of muscle fibers originating near the dorsal aspect of the premaxilla and maxillia course dorsally near the opening of the narial passages.

*M. Sphincter colli profundus pars oris* (SCPO) (Figure 18, C-F)

The *M. SCPO* runs in a rostro-caudal direction superficially on the upper and lower jaws. The muscle originates behind the angle of the mouth, and fans out to form a thick band on the lateral surface of the face, eventually blending with the *M. levator nasolabialis* and terminating in the skin of the snout. In the lower jaw, the *M. SCPO* runs rostrally from the angle of the mouth in a thin band adjacent and lateral to the *M. orbicularis oris*.

*M. Orbicularis oris* (Figure 18, D-F)

In the lower jaw, the muscle forms a distinct band that encircles the periphery of the lip just under the skin and medially to the *M. SCPO*. In the upper lip, the *M. orbicularis oris* is distinct from the angle of the mouth rostrally to the U2 bristle field, where it blends with the *M. buccinatorius*.

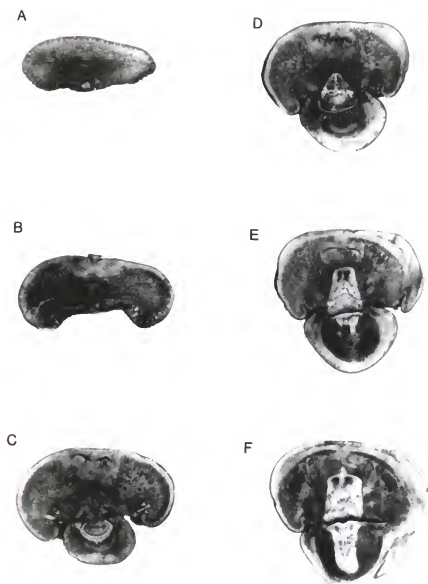
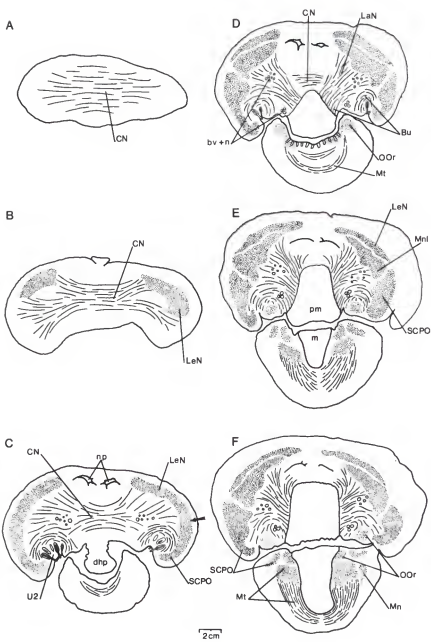


Figure 17. Photographs of the caudal surface of 2 cm coronal sections through the head. A-F represent a rostral to caudal sequence, respectively.

Figure 18. Schematic diagrams representing the caudal surface of 2 cm coronal sections (see Figure 17) representing the positions of facial muscles and other structures. Bu = M. buccinatorius, bv + n = blood vessels and nerves, CN = M. centralis nasi, dhp = dorsal hard palate, LaN = M. lateralis nasi, LeN = M. levator nasolabialis, m = mandible, Mn = M. mandibularis, Mnl = M. maxillonasolabialis, Mt = M. mentalis, np = narial passages, OOr = M. orbicularis oris, pm = premaxilla, SCPO = M. sphincter colli profundus pars oris, U2 = U2 bristle field,. Black arrows indicate the demarcation between the M. levator nasolabialis and M. SCPO.



*M. Mentalis* (Figure 18, D-F)

Originates on the dorsal border of the lateral surface of the mandible and runs in a broad sheet caudo-ventral to insert on a mid-sagittal plane on the skin of the lower jaw. Some slips of the muscle course in a rostro-caudal direction in the most rostral part of the jaw, and insert on the skin of the lower lip.

*M. Buccinatorius* (Figure 18, C-F)

Originates on the lateral surface of the premaxilla and maxilla, ventral to the origin of the *M. lateralis nasi*. The caudal portion of the muscle inserts on the alveolar border of the mandible. However, the rostral portion of the muscle courses rostrally to surround the U2 bristles and insert on the ventro-medial fascial surface of the *M. SCPO*. Fibers from the *M. lateralis nasi* blend with the *M. buccinatorius* as it projects laterally. Fibers from the *M. orbicularis oris* intersect with the *M. buccinatorius* immediately caudal to the U2 bristle fields.

*M. Maxillonasolabialis* (Figure 18, D-F)

Originates at the cranio-ventral border of the orbit. The fibers course rostro-caudally deep to the *M. levator nasolabialis* to insert on the dorsal region of the snout and onto the sides of the narial passages.

### Discussion

A number of investigators have described the rostral facial musculature of the genus *Trichechus*. Most of the facial myology appears to be fairly consistent across the species *T. inunguis*, *T. senegalensis* and *T. manatus*. Differences arise in the descriptions of the musculature of the rostral-most portion of the snout, and the area surrounding the U2 bristle fields of the upper lip.

In his description of the *M. lateralis nasi* of the Amazonian manatee, Domning (1978) noted that the nomenclature of the myology in this region remained unsatisfactory. I believe that the rostral portion of the muscle named *M. lateralis nasi* is actually a separate muscle, *M. centralis nasi*, with its most caudal portions arising from the premaxillary symphysis and fanning out cranially to insert on the skin of the snout. The distinctness of this muscle is



most evident in figure 2D. Gambaran and Souchanov (1986) give an illustration of the *M. lateralis nasi* that is consistent with Domning (1978), but in our observations, the direction of the muscle fibers is transverse in direction rather than dorso-ventral as illustrated in the other papers. In the more caudal portions of the *M. lateralis nasi*, our observations coincide with the descriptions and illustrations provided by previous investigators.

I also propose that the vibrissal-muscular complex of Florida manatees (and likely all trichechids if not all sirenians) is a muscular hydrostat as described by Kier and Smith (1985). Support systems of organisms are generally categorized as either (1) hardened skeletons, as in vertebrates and insects (internal skeletons or exoskeletons), or (2) hydrostatic skeletons in which the skeleton consists of a tough fiber-reinforced connective tissue container surrounded by a fluid filled cavity (e.g., polyps and annelids). Muscular hydrostats produce intricate, complex movements; these types of movement are much different than a lever-based hardened skeletal support system. Support for antagonistic actions of muscles in a lever-based, hardened skeletal system is provided by the skeletal elements (e.g., long bones). Such support in muscular hydrostats is provided by the muscles themselves and the fluid within the muscles. This type of support system allows for greater freedom of movement. Although many muscular hydrostats have skeletal attachments at the base, these skeletal elements do not provide support for antagonistic actions of muscle function and are therefore irrelevant in the function of a muscular hydrostat. Muscular hydrostats include whole organisms as well as parts of organisms (e.g. tentacles of squid, trunks of elephants, many types of tongues and lips). The snout of the manatee is comparable to these examples due to the paucity of skeletal elements used for

antagonistic support of facial muscles. Kier and Smith (1985) characterized muscular hydrostats as:

1. A three dimensional array of muscles in which the orientation of the muscles may lay in any plane relative to the long axis of the body (i.e. perpendicular, transverse, parallel, helical or oblique).
2. A structure of constant volume.
3. A capability to move in highly controlled, detailed and varied movements.

The three dimensionality of the musculature not only provides movement but also support for itself (Kier and Smith, 1985). The constant volume of these organs allows for diverse and highly controlled movements because a "change in one direction will cause a compensatory change in at least one other dimension" (Kier and Smith, 1985).

Principal movements of muscular hydrostats are elongation, shortening, bending and torsion. Elongation results from contraction of transverse, radial or circular muscles which have high length to width ratios. Shortening is a result of contraction of longitudinal muscle. Bending occurs when transverse and longitudinal or radial and circular muscles contract simultaneously. Torsion results from the shortening of helical or obliquely oriented muscles and can occur in both directions (Kier and Smith, 1985).

The oro-facial region of the Florida manatee fits many of the criteria of a muscular hydrostat. The manatees snout is a three dimensional array of muscles; due to the complexity of the manatee snout, our initial gross dissections were difficult and yielded little information until heads were sectioned and examined in cross section. Only then could information from gross dissections be interpreted correctly. Kier and Smith (1985) state that muscular hydrostats must be comprised mostly of muscle, although nerves, blood vessels or fat pads may be present. The only structures present rostral to the premaxilla bone and

mandible and deep to the dermis in Florida manatees are muscles, connective tissue, blood vessels, and nerves (see Chapter 2, Figure 10). Therefore, the manatee snout is a structure of constant volume. The diverse and highly controlled movements of the Florida manatee snout are documented in Chapter 3.

Facial muscles of the manatee snout are consistent with muscles types of a muscular hydrostat. Manatees possess the following type of muscles found in other examples of muscular hydrostats: transverse, radial, circular and longitudinal. The rostral extent of both right and left *M. Buccinatorius* forms a nearly circular muscle which extends the U2 bristle fields. Four of the eight facial muscles originate and insert on soft tissue components (*M. SCPO*, *M. Orbicularis oris*, *M. Centralis nasi*, and the rostral portion of the *M. Buccinatorius*). All other facial muscles originate on the skull but insert on soft tissue components. The extension of the premaxilla into the muscular hydrostat would slightly limit the ventral direction of movement of the perioral bristles. Instead of snout muscles having a full 360 degree range of motion in the transverse plane, the premaxilla likely limits the range of motion of the manatee snout to approximately 270 degrees. Qualitatively, the skin thickness surrounding the supradisk region (see Chapter 2 for definition) is much greater than the skin thickness of the oral disk. This difference in skin thickness facilitates the rostral direction of volume displacement and therefore allows elongation and extension of the U2 bristles to be maximized. The rostral extent of the lower jaw must also be taken into consideration. The *M. mentalis*, *M. sphincter colli profundus pars oris* (*SCPO*) and *M. orbicularis oris* all extend rostral to the mandibular symphysis to insert on soft tissue components and to create a small yet effective muscular hydrostat which everts the L1 bristle field.

Combining the anatomical data presented here and the behavioral data presented in Chapter 3, I propose the following functional assignments to the facial muscles described above, in the context of a muscular hydrostatic model. Each behavior presented in Chapter 3 will be explained in terms of this model.

### Submerged Vegetation

The sequence of behavior observed for manatees feeding upon submerged vegetation is broken down into five components as illustrated in Chapter 3 (Figure 15):

- A. Behavior: The most rostral muscular portion of the snout shortens rostro-caudally. This action pulls the oral disk dorsally and exposes the U2 bristles to the vegetation. I refer to this action as the "flare". There is a range of snout contraction observed.

Muscles: The upper lip area is likely to be pulled dorsally primarily by the contraction of the *M. levator nasolabialis* and *M. maxillonasolabialis*. Bristle extrusion to this point is considered to be muscularly passive, the result of the pull of the *M. levator nasolabialis* on the skin of the rostrum. This "flare" behavior is a result of contraction of longitudinal muscles (*M. levator nasolabialis*) or shortening as described by Kier and Smith (1985).

- B. Behavior: 1) The U2 bristles evert forward 2) then are moved medially to bring the plant material toward the midline of the body in a lateral to medial sweeping direction. 3) The lower jaw begins to open at this time.

Muscles: 1) The *M. buccinatorius* forms a semicircular muscular capsule around the relaxed, retracted U2 bristle bed. Contraction results in an extension of the bristles by volume displacement. When the bristles are fully erect, they protrude from a cone of connective tissue and muscle, at the base of which is the contracted *M. buccinatorius*. Maximal extension of the U2 bristles occurs with contraction of *M. buccinatorius* in conjunction with maximal snout shortening (see A above). In the context of a muscular hydrostatic contraction of a semicircular muscle (*M. buccinatorius*) results in elongation by definition (Kier and Smith 1985). In this case the elongation is limited to the U2 bristle field. In addition, the volume displacement of the U2 bristle field is enhanced by the compensatory change from the contraction of the *M. levator nasolabialis* as well as the *M. buccinatorius*. This additional volume displacement of the U2 bristles results from shortening a longitudinal muscle (*M. levator nasolabialis*). 2) The movement of the U2 bristle field to the midline of

the body is due to the contraction of the *M. centralis nasi*. 3) The lower jaw opens by contraction of the *M. digastricus* and the relaxation of *M. masseter* and *M. temporalis*. Lateral movement of the each U2 bristle field is achieved through contraction of the *M. sphincter colli profundus pars oris*, often antagonistically coordinated with the *M. lateralis nasi*.

- C. **Behavior:** 1) The right and left U2 bristles reach apposition at midline and push vegetation into the oral cavity; the lower jaw is now maximally open. 2) The L1 bristles evert from their fleshy pad.

**Muscles:** 1) Contraction of the *M. buccinatorius* maintains bristle protrusion (elongation); contraction of the *M. centralis nasi* pulls the bristle beds towards the midline, and a relaxation of the *M. SCPO* allows for a medial rotation of the cone. 2) Contraction of the *M. mentalis* results in the elongation of the connective tissue and perioral bristles of the L1 field. Our use of the term elongation here differs somewhat from that presented by Kier and Smith (1985) because the direction of muscle fibers and the action of elongation are rotated 90 degrees relative to the long axis of the body. The lower lip region of the Florida manatee is surrounded by a thick and tough skin which acts to help direct the movement of the L1 bristle field dorsally.

- D. **Behavior:** 1) The U2 bristles diverge laterally and 2) the lower jaw begins to close.

**Muscles:** 1) The lateral movement of the bristles is the result of the contraction of the *M. SCPO* and the relaxation of the *M. centralis nasi*. The bristles begin to retract as the *M. buccinatorius* relaxes and allows the bristles to return to their resting positions in the fleshy folds of the

upper lip. 2) Contraction of the *M. masseter* and *M. temporalis* muscle are responsible for the closing of the jaw.

- E. **Behavior:** 1) As the lower jaw closes the L1 bristle field sweeps vegetation caudally into the mouth. 2) The U2 bristles arrive at their original and lateral position. 3) A new grasping event then begins.

**Muscles:** 1) Contraction of the *M. orbicularis oris* pulls the L1 bristle field in towards the oral cavity over the rim of the mandible. 2) Continued relaxation of *M. centralis nasi* and continued contraction of *M. SCPO* brings the U2 bristle fields back to their original position. 3) The *M. buccinatorius* begins to contract.

I propose a model of sequential muscle activation which is correlated with the submerged feeding behavior described in Chapter 3 and depicted in Figure 19. A direct test of this model could be made using electromyography (EMG) data. However, such data do not exist.

### Floating Vegetation

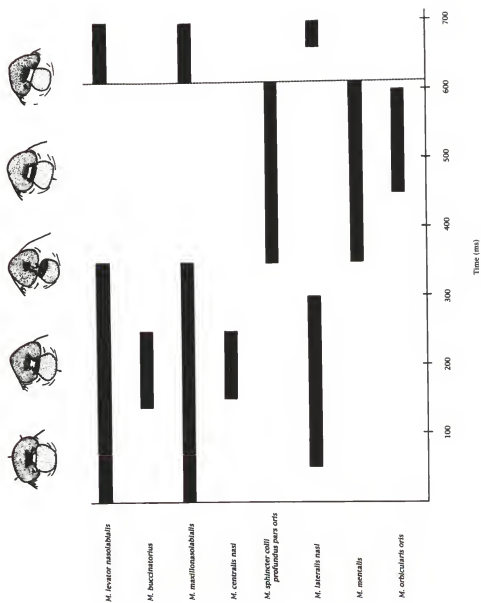
- A. Behavior: The U2 bristle fields are often used individually or together in a rostro-caudal raking fashion, distinct from the typical feeding pattern described above. The upper lip(s) reach out for the vegetation with the upper bristles extended and pointed downward. The individual then reaches for the vegetation and attempts to drag it closer to the mouth.

Muscle: Detailed observation of an individual manatee using the right or left U2 bristle field independently reveals that the degree of extension is quite remarkable. The swelling and extension on that side of the snout which is in use is also accompanied by contraction of the majority of the facial muscles on the contralateral side. If both U2 bristle fields are used in such an extension, then a narrowing of the snout is observed. I have stated that elongation results from contraction of transverse, radial or circular muscle. The *M. lateralis nasi* is oriented transversely to the long axis of the body. Contraction of this muscle would produce a narrowing of the snout at the level of the tip of the premaxilla. The corresponding compensatory change in volume would extend the region rostral to the site of contraction parallel to the long axis of the body. Such behavior may explain reports in the older literature which suggested that the snout of manatees was composed of erectile tissue (Garrod 1879).

### Other Manipulative Behaviors

Various combinations of muscular hydrostatic elongation, shortening and bending may produce many of the diverse behaviors observed, including independent use of the U2 and L1 bristle fields during feeding and exploration. *M. centralis nasi* and *M. orbicularis oris* appear to make little contribution to the muscular hydrostat during feeding but are still integral for performing various behaviors. For instance, the action of bringing the U2 bristles together at the midline so that they meet or are overlapped at the midline is likely to be controlled by the *M. centralis nasi*. Although the extension of the U2 bristles is a result of elongation, once extended, the movement of the U2 bristle fields themselves does not exhibit further elongation, but only movement in other directions, and therefore is not a hydrostatic characteristic. Similarly, reversal

Figure 19. Proposed summary of muscle time course correlated with feeding behavior model (submerged vegetation). Schematic of manatee feeding behavior is taken from Chapter 3. Dotted line indicates mean feeding cycle length of 610 ms (Chapter 3).





of the direction of the movement of the U2 bristles is likely not a hydrostatic event, except for the elongation of the bristles themselves. The same is likely true for the independent use of the L1 field; the *M. orbicularis oris* and *M. mentalis* do not exhibit strong hydrostatic characteristics beyond elongation to produce the eversion of the perioral bristles. However, exploratory behavior is likely to exhibit many hydrostatic characteristics. Many quick, small movements from side to side and up and down are likely the result of alternate contractions of left vs. right longitudinal muscles creating alternate patterns of elongation and shortening through the principle of compensatory change for each muscular contraction.

Comparative studies of facial muscles have shown that over a large range of mammalian taxa which possess prominent muscular-vibrissal complexes, specific facial muscles are associated with the movement of specific fields of vibrissae (Huber 1930a, 1930b). Generally the movements of mystacial vibrissae are manipulated by *M. maxillonasolabialis* and *M. levator nasolabialis*, mental vibrissae are controlled by *M. mentalis*, supraorbital vibrissae are moved by *M. depressor supercillii* and the genal vibrissae are moved in part by the *M. platysma* and *M. sphincter colli profundus pars oris* (SCPO).

The presumed involvement of the *M. levator nasolabialis* in the protrusion of the U2 bristles also supports my previous contention that the U2 bristles are homologous to the mystacial vibrissae (Chapter/2) of the common mammalian plan described by Huber (1930a). Accordingly, the L1 bristle field is presumed to be protruded by contraction of the mentalis muscle and therefore I hypothesize that this field of bristles is homologous to the mental vibrissae of other mammals.

## CHAPTER 5

### VARIATION OF FEEDING CYCLE DURATION OF FLORIDA MANATEES FEEDING ON SEVERAL SPECIES OF AQUATIC VEGETATION

#### Introduction

Among mammals, sirenians are unique in that perioral bristles are used in a prehensile manner in conjunction with complex facial movements to bring vegetation into the mouth (Chapters 2 through 4). As generalist feeders, Florida manatees consume a wide variety of aquatic vegetation. How is the manatee vibrissal-muscular complex able to manipulate the range of structural varieties represented by the wide variety of plants? It is the objective of this study to examine manatees feeding upon several species of plants which represent a wide range of variation which manatees consume in the wild. I hypothesize that manatees will handle these types of vegetation differently as reflected in differences in the duration of the feeding cycle length. These hypothesized differences would effect consumption rates.

#### Methods

##### Feeding Trials

Feeding trials on captive manatees were conducted at three facilities, Homosassa Springs State Park (HSP), Homosassa, FL; Lowry Park Zoological Gardens (LPZ) in Tampa, FL; and Sea World of Florida (SWF), Orlando, FL. A total of seventeen animals, five females and twelve males, were used in this study.

Three species of freshwater vegetation: *Hydrilla verticillata* (Hydrilla), *Myriophyllum spicatum* (eurasian watermilfoil), *Vallisneria americana* (tapegrass or wild celery), and two species of seagrass, *Syringodium filiforme* (manatee grass) and *Thalassia testudinum* (turtle grass) were fed to manatees. A feeding trial consisted of presenting one species of aquatic plant to captive manatees using a plexiglass feeder (which is described below and in Chapter 3); an individual was required to consume approximately 80 to 90% of all vegetation presented in order to complete a single feeding trial. All vegetation used in this study are species normally consumed by free ranging Florida manatees. Feeding trials were conducted in order to obtain data on the major components of the feeding cycle (Chapter 3) as well as to obtain quantitative data regarding the duration of the feeding cycle (this study). Presentation of vegetation to manatees has been described in detail previously (Chapter 3). However, a short summary is provided here.

Feeding trials were conducted between May and August in 1993, 1994, and 1995. A total of 372 feeding trials were conducted over this time period. Trials involved novel food for captive manatees and they found them preferable to their normal diet. Satiation of individuals did appear to be a problem.

Preliminary trials (1993) were conducted using five males (LPZ) and five females (HSP) during which 120 feeding trials were conducted. During these feeding trials, only freshwater vegetation (*Hydrilla*, *Myriophyllum* and *Vallisneria*) was presented without regard to order and on a "first come, first served" basis.

Feeding trials during 1994 were conducted with three males (LPZ) and three females (HSP). Two hundred seventy nine trials were conducted in a statistically balanced research plan for a total of ten weeks at LPZ and for nine weeks at HSP. All trials were conducted once a week at each facility between 900

and 1500 hours. All five species of vegetation were presented to each individual during these experiments. I attempted to control the order in which aquatic vegetation was presented to specific individuals. An ordered sequence of feeding trial presentations helps to ensure that any vegetation type has an equal chance of being in any presentation to a given manatee. This also prevents a systematic bias due to an ordering effect. The sequence in which each vegetation was presented was changed for each daily session. Also, because each vegetation is presented to each animal during each day feeding trials were conducted, each feeding trial day is statistically a random blocking design.

Feeding trials (N=49) were conducted at SWF during 1995. Five male manatees were presented with the same feeding regime as in the 1994 feeding trials; all vegetation species were presented to all individuals involved on any particular data collection day. Due to limited resources and release of several captive manatees at this facility, individuals were sampled only twice over a five week period.

During 1993 at HSP and LPZ, and 1994 at LPZ, vegetation was presented to manatees on a square sheet of plexiglass (approximately 80 cm x 90 cm) with holes drilled at 10 cm intervals. Pieces of vegetation were pushed into the holes and the plexiglass was placed on an underwater viewing window using suction cups. Feeding trials at HSP in 1993 and SWF (1995) utilized a mobile underwater window (MUW) constructed of PVC (Figure 11). This apparatus also held an underwater videocamera and video housing (Yashica model KD-H170u Hi8 format; Amphibico housing) which recorded manatees feeding from the plexiglass.

Videotape analysis consisted of quantification of the duration of each manatee feeding cycle (as defined in Chapter 3) for each individual feeding

upon each species of submerged vegetation. Frame by frame analysis was conducted using S-VHS backup tapes and a Panasonic model AG-7300 S-VHS editor in conjunction with either an IBAS computer imaging system (Kontron Image Analysis Division) which supported a black and white imaging monitor or a Sony Trinitron model PVM-1350 color video monitor. Feeding trials at LPZ and HSP during 1994 were conducted under a statistically balanced research design. A multivariate analysis of variance (MANOVA) and univariate analysis of variance (ANOVA) were used to evaluate differences among mean feeding cycle lengths and vegetation. Fisher's Least Squared Difference (LSD) post-hoc tests were used to evaluate differences in mean feeding cycle length and species of vegetation. Feeding trials conducted at SWF were not included in the MANOVA. Data from SWF manatees were used as adjunct data to test my hypothesis regarding the effects of study sites, gender and body length on manatee feeding cycle duration.

### Results

The mean feeding cycle length (as defined in Chapter 3) of all subjects feeding on all vegetation from all trials (1993, 1994 and 1995) was 610 ms (S.D.  $\pm$  52.9). Feeding cycle length of Florida manatees feeding on all plant species ranged from 473 to 745 ms. Manatees eating *Hydrilla* possessed the shortest feeding cycle lengths, followed by *Myriophyllum*, *Vallisneria*, *Syringodium* and finally *Thalassia* (longest feeding cycle length)(Figure 20). A non-repeated measure analysis of variance (ANOVA) revealed a significant interaction between mean feeding cycle and vegetation ( $p < .0001$ ).

Fisher's LSD post-hoc pair-wise test revealed significant differences between all vegetation species except between *Hydrilla* and *Myriophyllum* and between *Syringodium* and *Vallisneria* (Table 4).

Overall, males had a shorter mean feeding cycle length than females (Figure 21). The mean feeding cycle length for males and females were 596 ms (S.D.  $\pm$  56.2) 631 ms (S.D.  $\pm$  39.0), respectively. Male feeding cycle lengths ranged from 373 ms to 745 ms. Female cycle lengths ranged from 553 ms to 740 ms. This gender difference in mean feeding cycle length is statistically significant

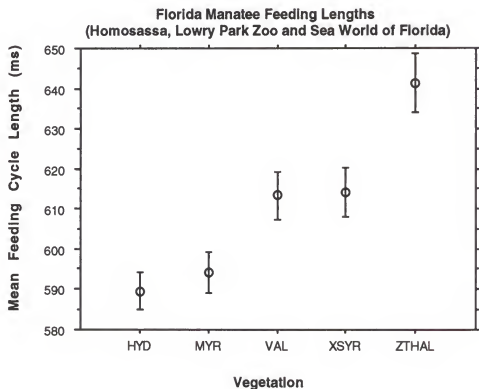


Figure 20. Feeding cycle lengths of manatees feeding on submerged plant species. Each data point is a mean for all individuals (N=17). HYD = *Hydrilla verticillata* (Hydrilla), MYR = *Myriophyllum spicatum* (eurasian watermilfoil), VAL = *Vallisneria americana* (tapegrass or wild celery), XSYR = *Syringodium filiforme* (manatee grass) and ZTHAL = *Thalassia testudinum* (turtle grass). Bars =  $\pm$  1 standard error.

Table 4: Fisher's LSD Post-hoc Pair-wise Comparison of Vegetation and Mean Feeding Cycle Length (Significance Level = 5%)

	Mean Diff.	Crit. Diff	P-Value	
HYD, MYR	-4.636	15.720	.5623	
HYD, SYR	-24.496	16.492	.0037	S
HYD, VAL	-23.738	15.479	.0027	S
HYD, ZTHAL	-51.736	16.356	<.0001	S
MYR, SYR	-19.860	16.539	.0187	S
MYR, VAL	-19.102	15.530	.0161	S
MYR, ZTHAL	-47.100	16.404	<.0001	S
SYR, VAL	.758	16.311	.9272	
SYR, ZTHAL	-27.241	17.145	.0019	S
VAL, ZTHAL	-27.999	16.174	.0007	S

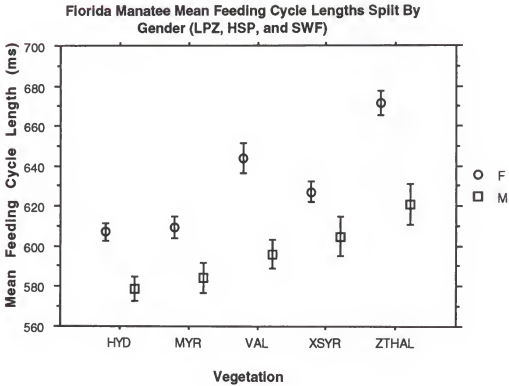


Figure 21. Feeding cycle lengths for male and female manatees feeding on submerged plant species. Each data point is a mean for all individuals (N=17, 5 females, 12 males). HYD = *Hydrilla verticillata* (Hydrilla), MYR = *Myriophyllum spicatum* (eurasian watermilfoil), VAL = *Vallisneria americana* (tapegrass or wild celery), XSYR = *Syringodium filiforme* (manatee grass) and ZTHAL = *Thalassia testudinum* (turtle grass). Bars =  $\pm$  1 standard error.

at the  $p < .0001$  level (unpaired t-test). In contrast to the male pattern, the mean feeding cycle length for females manatees consuming *Syringodium* was shorter than when consuming *Vallisneria*.

#### LPZ and HSP 1994

Experimental feeding trials were completed with three males at LPZ and three females at HSP in a statistically balanced design over a nine week period during the summer of 1994. The mean feeding cycle length was 620 ms (S.D.  $\pm$  48.02) and ranged from 493 ms to 745 ms (Figure 22).

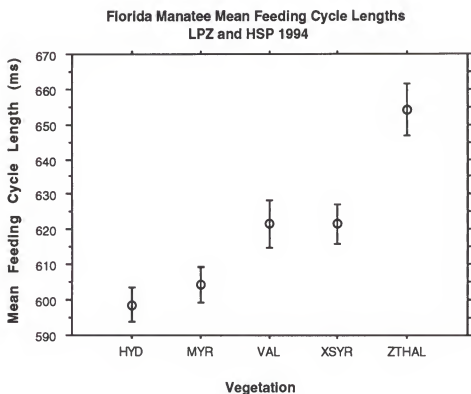


Figure 22. Feeding cycle rates for manatees feeding on submerged plant species during the 1994 study. Each data point is a mean for all individuals (N=6). HYD = *Hydrilla verticillata* (Hydrilla), MYR = *Myriophyllum spicatum* (eurasian watermilfoil), VAL = *Vallisneria americana* (tapegrass or wild celery), XSYR = *Syringodium filiforme* (manatee grass) and ZTHAL = *Thalassia testudinum* (turtle grass). Bars =  $\pm$  1 standard error.



With respect to variations in cycle length with vegetation type, I observed a similar trend as described for the entire pooled study. Individuals feeding upon *Hydrilla* possessed the shortest mean feeding cycle length (599 ms), followed by *Myriophyllum* (604 ms), *Vallisneria* (622 ms), *Syringodium* (622 ms), and lastly, *Thalassia*. (654 ms). The balanced design of this study allowed a multivariate analysis of variance (MANOVA) to be performed. The MANOVA examined the following variables: mean feeding cycle length vegetation, site, gender and body length. A significant interactions were shown for mean feeding cycle and vegetation and for mean feeding cycle and study site. Individual post-hoc t-test (Fisher's LSD) showed significant difference between all mean feeding cycle length and all species of vegetation except for *Hydrilla* and *Myriophyllum* and *Vallisneria* and *Syringodium*. (Table 5).

Table 5: Fisher's LSD Post-hoc Pair-wise Comparison of Vegetation and Mean Feeding Cycle Length for LPZ and HSP 1994 (Significance Level = 5%)

	Mean Diff.	Crit. Diff	P-Value	
HYD, MYR	-5.685	16.766	.5049	
HYD, VAL	-22.969	16.766	.0074	S
HYD, XSYR	-23.025	16.766	.0073	S
HYD, ZTHAL	-55.574	16.766	<.0001	S
MYR, VAL	-17.284	16.766	.0434	S
MYR, XSYR	-17.339	16.766	.0427	S
MYR, ZTHAL	-49.889	16.766	<.0001	S
VAL, XSYR	-.056	16.766	.9948	
VAL, ZTHAL	-32.605	16.766	.0002	S
XSYR, ZTHAL	-32.549	16.766	.0002	S

Differences in gender were also significant ( $p < .0001$ , unpaired t-test) in this study. Mean male and female feeding cycle lengths were 608 (S.D.  $\pm 54.2$ ) and 631 (S.D.  $\pm 36.2$ ), respectively (Figure 23). Again, females (HSP) feeding on

*Vallisneria* had a longer mean feeding cycle length than when feeding on *Syringodium* compared to their LPZ counterparts. Overall, females had a significantly longer mean feeding cycle length than males (Figure 23).

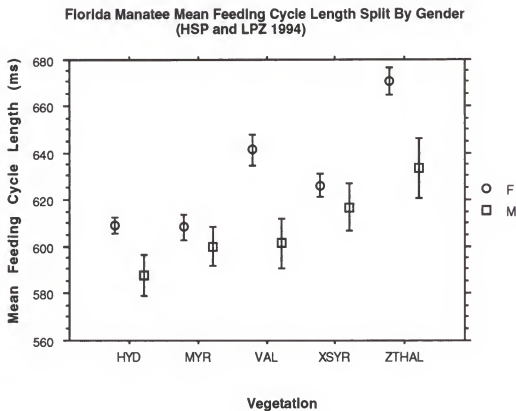


Figure 23. Feeding cycle rates for each gender of manatees feeding on submerged plant species during the 1994 study. Each data point is a mean for all individuals (N=6, 3 males and 3 females). HYD = *Hydrilla verticillata* (Hydrilla), MYR = *Myriophyllum spicatum* (eurasian watermilfoil), VAL = *Vallisneria americana* (tapegrass or wild celery), XSYR = *Syringodium filiforme* (manatee grass) and ZTHAL = *Thalassia testudinum* (turtle grass). Bars =  $\pm 1$  standard error.

#### SWF 1995

Individuals from the third site (SWF) were sampled during the summer of 1995. The mean feeding cycle length for SWF subjects was 560 ms (S.D.  $\pm 51.2$ )

and ranged from 473 to 675 (Figure 24). I observed a similar trend from shortest to longest mean feeding cycle lengths of vegetation as reported for LPZ and HSP (*Hydrilla*, *Myriophyllum*, *Vallisneria*, *Syringodium*, *Thalassia*). Analysis of variance showed no significant interaction between mean feeding cycle length and species of vegetation ( $p=.88$ ). This is likely a function of the small sample size and limited sampling of the SWF population.

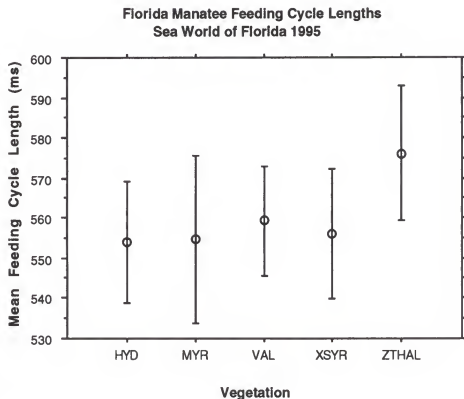


Figure 24. Feeding cycle rates for manatees feeding on submerged plant species during the 1995 study. Each data point is a mean for all individuals ( $N=5$ ). HYD = *Hydrilla verticillata* (Hydrilla), MYR = *Myriophyllum spicatum* (eurasian watermilfoil), VAL = *Vallisneria americana* (tapegrass or wild celery), XSYR = *Syringodium filiforme* (manatee grass) and ZTHAL = *Thalassia testudinum* (turtle grass). Bars =  $\pm 1$  standard error

### Gender and Body Size

A comparison of all three sites (Figure 25) shows differences in mean body length among the three study sites and differences in mean feeding cycle length between each site. These differences were significant for each pairwise comparison ( $p < 0.05$ , unpaired t-test in each case). Therefore the effect of gender on feeding cycle length is confounded with effects of body length. Mean body lengths and feeding cycle lengths were longest at HSP, followed by LPZ then SWF (Figure, 25). To draw out differences between gender and body

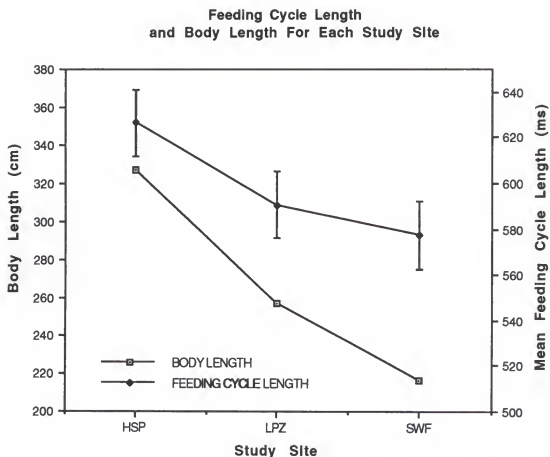


Figure 25. Mean feeding cycle lengths compared to mean body length for each site were significantly different. Each data point is a mean of feeding trials for all individuals at that site ( $N=372$ : HSP=151, LPZ=172, SWF=49). Bars =  $\pm 1$  standard error.

length it is useful to examine mean body weight length and mean feeding cycle length in males at the two different study sites (LPZ and SWF). Pair-wise comparison of mean body length between the two sites shows a significant difference ( $p < 0.05$ ); LPZ male are longer than SWF males. Mean feeding cycle between LPZ (605 ms) and SWF (560 ms) was also significantly different ( $p < 0.05$ ). LPZ males, which were longer in body length than SWF males SWF, had a greater mean feeding cycle length compared to SWF males. Therefore, mean feeding cycle length would appear to be independent of gender but dependent on mean body length. Regression analysis of mean feeding cycle rate and mean body length shows a linear correlation between these two variables ( $r^2 = 0.54$ ) (Figure 26). The SWF individuals were not included in the regression analysis

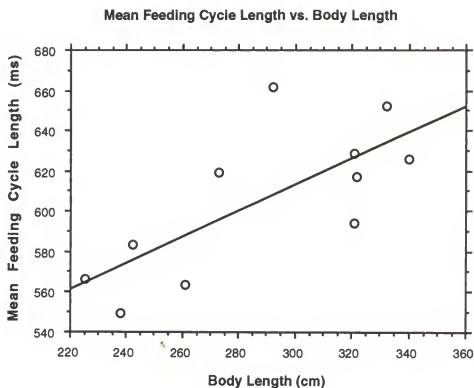


Figure 26: Predictive value for estimating mean feeding cycle length from body length in Florida manatee. Each data point equals the mean feeding cycle length for an individual of that particular body length. Body length is predictive of feeding cycle length at the  $r^2 = .54$  ( $Y = 419.648 + .646 * X$ ;  $r^2 = .54$ ,  $N=11$ ).

due to the limited sampling and high variability of feeding cycle rates which are likely associated with small sample size.

### Discussion

Since chewing requires that food be present in the oral cavity, it is intuitive that manipulation and introduction of food into the oral cavity are intimately linked with mastication. Indeed, the mean feeding cycle length of 610 ms reported in this studies corresponds to 1.64 chews per second which falls between chewing rate values reported by Bengtson (1983) and Etheridge *et al.* (1985)(Table 6). Chewing rates and mean feeding cycle lengths may constrain processing of food (mastication). For example, manatees feeding upon aquatic plants in this study were observed to introduce vegetation into the oral cavity without interruption. This may be interpreted to imply that, the aquatic plants presented were processed as fast as, or faster than the introduction of food into the mouth. In contrast, manatees feeding on non-aquatic foods, such as carrots, were observed to introduce food into the oral cavity for a certain time period then stop; at this time chewing was observed to continue (audible). I interpret this behavior as the introduction of food into the oral cavity exceeding the rate of food processing. Food must be chewed further before introduction of additional food can occur. Therefore, mastication can be rate limiting. Manatees feeding upon aquatic vegetation were never observed to interrupt introduction of food into the oral cavity. It would appear that processing of aquatic plants used in this study was not rate limiting. Differences observed in mean feeding cycle lengths of manatees feeding upon a variety of aquatic plants suggest that introduction of plants into the oral cavity may also be rate limiting. The data show a consistent trend so that certain plants are handled

and introduced into the mouth faster than others. I hypothesize that plant morphology may be one of many factors which can limit feeding rates. Other factors such as fiber content, plant anatomy and biomechanical properties may also effect handling time and, therefore, food processing rates.

Table 6: Summary of Manatee Feeding Data

<u>REPORT</u>	<u>"CHEWS PER SECOND"</u>	<u>"FEEDING CYCLE LENGTH"</u>
Bengtson (1983)	1.05	952*
Marshall (this study)	1.64 <sup>+</sup>	610
Etheridge <i>et al.</i> (1985)	1.86	537*

<sup>+</sup>Calculated from feeding cycle length

\*Calculated from chews per second.

Etheridge *et al.* (1985) reported rates of chewing from wild and captive manatees. The pooled mean rate for manatees feeding upon *Hydrilla* and *Vallisneria* in that study was 1.86 chews per second (538 ms). Mean chew rates between captive and free-ranging manatees were found to be similar. In addition, they reported that the mean number of chews required to consume *Hydrilla* varied inversely with body weight. Etheridge *et al.* (1985) attributed the differences in chew rates for animals of different body size to, calves having a smaller grinding surface area (teeth) and chewing faster than adults. Calves must chew many more times to consume the same amount of food as adults. One captive manatee was fed *Vallisneria*; consuming *Vallisneria* required many more chews per unit time compared to *Hydrilla*.

Although it may be true that calves must chew faster to consume the same amount of food as adults, and calves do have smaller grinding surface area compared to adults, it is also likely that differences in the correlation of body length with feeding rates may also be related to the allometric increase in size of the oral disk (including perioral bristles). For example, the area of the oral

disk is strongly correlated with body weight and length (Chapter 2, Figure 9;  $r^2=0.86$ ). As the oral disk increases in size, the distance between the U2 bristle fields (which may be compared to gape) also increases. The increase in size of the oral disk may affect the timing of the mechanics of feeding and, therefore, the handling time of vegetation.

Bengtson's (1983) calculations were based on manatees feeding upon water hyacinth (*Eichhornia crassipes*), water lettuce (*Pistia stratiotes*) and wild celery (*Vallisneria americana*). Calculations made by Etheridge *et al.* (1985) were based on manatees feeding on *Hydrilla* and some *Vallisneria*. Feeding rates calculated from mean feeding cycle lengths reported in this study not only fall between those values reported by Bengtson (1983) and Etheridge *et al.* (1985) but are close to the mean of these two studies (1.45 chews per second). Calculations in this report (Tables 6 and 7) are based on manatees feeding upon a variety of aquatic

Table 7: Feeding Data for Each Species of Vegetation

VEGETATION	<u>FEEDING CYCLE LENGTH(ms)</u>	<u>CHEWS PER SECOND</u>
<i>Hydrilla</i>	590	1.69*
<i>Myriophyllum</i>	594	1.68*
<i>Vallisneria</i>	613	1.63*
<i>Syringodium</i>	614	1.62*
<i>Thalassia</i>	641	1.56*

\*Calculated from feeding cycle lengths (chews per second =  $1/\text{mean feeding cycle length} \times 1000$ ). Mean feeding cycle length = 610 ms. Mean chews per second = 1.64.

vegetation (three freshwater and two marine species), including species examined by both Bengtson (1983) and Etheridge *et al.* (1985). This study suggests that a spectrum of feeding rates exists which may be dependent upon the inherent characteristics of each species of aquatic plants being consumed.



## CHAPTER 6 EVOLUTIONARY IMPLICATIONS OF SIRENIAN FEEDING BEHAVIOR: A COMPARATIVE VIEWPOINT

### Introduction

Aquatic herbivory is an outlier among mammalian feeding niches. Mammals have radiated to fill numerous niches and a diverse number of terrestrial herbivores exist. However, of the three taxonomic groups of marine mammals (Order Cetacea; Order Carnivora, Suborder Pinnipedia and Order Sirenia), only the Sirenia have exploited aquatic angiosperms. Of the sirenians, only the dugong is exclusively marine (Anderson, 1979). Steller's Sea Cow (*Hydrodamalis gigas*), also a dugongid, was also exclusively marine and unusual among Recent sirenians in that it inhabited cold waters. It was recently hunted into extinction (circa 1768)(Domning, 1987; Reynolds and Odell, 1991).

Sirenians were much more diverse during the Miocene; numerous dugongid species dominated the Caribbean region until the Eocene, when trichechids apparently displaced dugongids completely (Domning, 1982). Dugongs are now absent from the new world. Domning (1982) speculated that this may have occurred due to differences in rostral deflection and tooth morphology and in the ways in which these factors effect sirenian feeding ecology.

The functional significance of rostral deflection in sirenians appears to be related to feeding ecology. The Amazonian manatee feeds mainly upon natant vegetation and therefore a snout with little downward reflection would be most adaptive (Domning, 1982). That the rostral angle of West African

manatees is slightly less than West Indian manatees could be due to the fact that *T. senegalensis* feed more on natant vegetation compared to *T. manatus*. Even so, the intermediate deflections of *T. manatus* and *T. senegalensis* suggest a compromise in adapting to their more generalized feeding niches. Benthic feeding is made energetically less expensive by a sharply downturned rostrum which orients the mouth to the bottom (Domning, 1976; Domning and Hayek, 1986). Behavioral tests performed on Amazonian and West Indian manatees appear to support this hypothesis (Domning, 1980).

Manatees and dugongs have different tooth morphologies. Domning (1982) speculated that the evolution of supernumerary teeth by trichechids may have allowed them to out-compete dugongs, which have open rooted, peg-like teeth. Manatee teeth are unusual compared to most other mammals. Teeth are limited to molars. Manatee dentition, in general, is bilophodont with an enameled edge (Domning and Hayek, 1984). New teeth are erupted in the rear of the jaw and migrate forward as wear on the teeth progresses. As teeth wear, they migrate to the front of the jaw and are shed, analogous to a conveyor belt (Domning, 1982; Domning, 1983). The mechanism behind this forward progression of teeth is the constant re-absorption of bony septae between the roots of the teeth and re-deposition of the bony septae under pressure of the forward moving teeth (Domning, 1983; Domning and Hayek, 1986). Re-absorption and re-deposition must occur simultaneously at a slow but continuing pace. Forward progression is about one or two millimeters per month. All teeth are connected by longitudinal strong fibers which help pull new teeth forward. Only the elephant and rock wallabies have a similar system (Roth and Shoshani, 1988; Sanson, 1989). Both manatees and rock wallabies have an unlimited number of supernumerary teeth that can be replaced (Domning, 1982; Sanson, 1989). However, elephants possess the usual

complement of mammalian teeth for their Family and do not have the ability to generate more. In addition, only a few teeth are erupted at one time which allows elephants to prolong the life of its teeth. Dugongs do not possess this conveyor belt system of tooth replacement. Instead, dugongs possess simple, rootless, peg-like cheek-teeth with tuberculated crowns which wear and appear to lose the surface enamel before or shortly after eruption (Domning, 1982; Marsh, 1980). Dugong molars do erupt at different time in manner similar to elephants (Lanyon, 1991). Some forward progression has been mentioned in the literature but this is minimal and has been attributed to normal "mesal drift" of mammalian dentition (Domning and Hayek, 1984). There may be some axonal and radial growth of cheek-teeth as dugongs mature (Marsh, 1980).

Lanyon (1991) speculated that dugong teeth are non-functional and that instead they use the enlarged upper and lower cornified horny pads of the downturned rostrum to grind food. This conjecture is based on the high variability of cheek-teeth size, compared to low variability of the horny pad size. Dugongs feed primarily upon seagrasses, which are known to have little abrasive characteristics compared to grasses. Therefore, Lanyon argued that there is no need for adaptations of dentition as are present in manatees. Although dugongs do consume rhizomes of seagrasses, compensation for increased wear on teeth from sand and sediment is explained by radial and axial growth of teeth. Theoretically, this would reduce selection pressure for a mechanism that replaces teeth as in trichechids.

Herbivores have evolved several solutions to tooth wear. Horses possess hypsodont teeth; the higher crown simply takes longer to wear down (Vaughn, 1986, p. 191). Other terrestrial herbivores have evolved cheek-teeth which are rootless and therefore continue to grow as the crown is worn down (DeBlase and Martin, 1981, p. 21). At one time dugongids possessed rooted cheek-teeth,

however, *Dugong* evolved rootless cheek-teeth and delayed eruption of teeth possibly as an adaptation to abrasive vegetation (Domning, 1982). Although the hypothesis promoted by Lanyon (1991) that dugong teeth are totally non-functional seems unlikely, the upper cornified horny pad may prove to be used to a greater extent in dugongs than manatees. This enlarged horny pad in dugongs may be a recent adaptation for an obligate seagrass herbivore used in conjunction with cheek-teeth and allowing dugongs to exploit a wider variety of food by increasing the efficiency with which seagrass is processed.

The function of perioral bristles in dugongs and the mechanism for harvesting seagrass has largely been ignored. This is due, in part, to the difficulty of making direct observations of mouth-to-benthic interactions. Dugongs release large amounts of silt into the water column when feeding. Even observations of dugongs feeding in good water conditions, such as those in Vanuatu (Oceania; northeast of New Caledonia), have failed to visualize the process of introducing seagrasses into the mouth. "There is no definitive account of how dugongs actually ingest seagrass. Their retiring nature and habit of stirring clouds of sediment when feeding have conspired to prevent any revealing underwater observations in the wild." (Preen, 1992). Even so, Domning (1977) and Anderson (1979) do provide brief accounts on the function of the oral disk musculature and the perioral bristles during feeding.

Manatees use modified vibrissae (perioral bristles) in combination with complex facial musculature to grasp vegetation and introduce it into the oral cavity (Chapter 3). This use of vibrissae in a prehensile manner is unique among mammals and perhaps vertebrates. The form, distribution, innervation, behavioral use, and functional model of perioral bristles have recently been systematically investigated for Florida manatees (Chapters 2 through 4). The objective of the present investigation was to compare the behavioral use of

perioral bristles by dugongs with data known for Florida manatees. Also, observations of perioral bristle use in Amazonian manatees and Antillean manatees have been made, and will be contrasted and compared with data on Florida manatees and dugongs.

### Methods

Feeding behavior of two dugongs (one male, one female) was observed in captivity at the Toba Aquarium in Toba City, Japan (Mie Prefecture). The feeding behavior of one Amazonian manatee (female) and one Antillean manatee (male) was observed at the Yomiuriland Marine Aquarium in Tokyo, Japan.

### Dugongs

The Toba Aquarium, located in Toba City, Japan (Mie Prefecture) has maintained dugongs since 1977 (Anonymous, 1995). Dugongs kept at the Toba Aquarium are maintained on *Zostera marina* (eel grass) a temperate to sub-tropical seagrass. Dugongs feed upon *Z. marina* in the wild (Preen, 1992). The behavioral use of perioral bristles by feeding dugongs was examined using a slight modification of methods outlined in Chapters 3 and 4. A plexiglass apparatus attached to an underwater viewing window with suction cups was used to present dugongs with seagrass (Figure 27). Holes were drilled through the plexiglass at 10 cm intervals and blades of seagrasses were partially pushed through the holes. In the case of the dugong apparatus, a rectangular piece of plexiglass was bent through the middle from its long side to long side to form a ninety degree angle. Single parallel bends were made at approximately 10 cm

from each end; these bends were 120 degrees each. These last two bends served as a flange onto which the suction cups were attached and therefore were positioned parallel to the viewing window. Sides were added to provide additional strength. In this manner, seagrass could be presented to dugongs at a 45° angle. Such an angle provided a simple yet effective compromise between the dugong's preferred feeding position of zero degrees (to the horizontal plane) and the preferred filming position of 90 degrees. In addition, dugongs were videotaped feeding upon free floating seagrass using the underwater video camera alone to determine if differences existed between feeding upon floating versus submerged vegetation.

Feeding trials were first conducted with the female dugong named Serena. Serena was captured in the Philippines as a calf and hand reared, and was therefore relatively docile. Feeding trials were conducted between 0800 and 1300 hours from 04 Jan 95 to 18 Jan 95. The plexiglass apparatus was filled with vegetation and placed on an underwater viewing window approximately 2 meters above the holding tank bottom by an assistant using SCUBA. Serena declined to feed from the apparatus until her morning feeding regime was suspended. Data were first collected on 07 Jan 95 and every day thereafter until 18 Jan 95. Both sides of the apparatus were filled with the vegetation; after the dugong had fed from the top side, the apparatus was simply turned 180 degrees and another trial commenced. Feeding trials with the male dugong, Jun-Ichi were conducted only after the Toba Aquarium Dugong Staff felt satisfied that the feeding apparatus was working. These feeding trials were conducted from 10 Jan 95 to 18 Jan 95 immediately following the feeding trials with the female dugong. This usually occurred on or about 1000 hours. The morning feeding regime was normally suspended during feeding trials to encourage the dugong to feed on the plexiglass apparatus. Satiation of individuals was not a problem

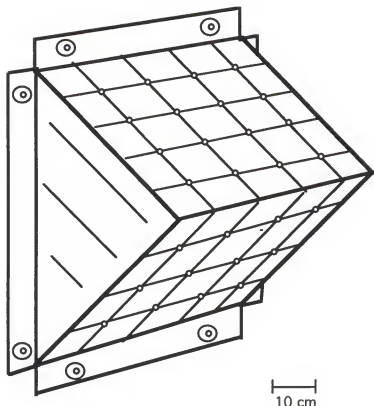


Figure 27. Feeding apparatus used to present seagrasses to captive dugongs. The plexiglass is constructed so that the seagrass is presented at a 45 degree angle.

and both dugongs appeared to be hungry prior to and during the feeding trials. This was evidenced by both dugongs searching and consuming stray seagrass leaves floating in the tank prior to the feeding trials and rapidly consuming their morning allowance of seagrass following the feeding trials.

#### Amazonian and Antillean Manatees

Collection of data on behavioral use of perioral bristles by the Amazonian and Antillean manatees was also made in a manner similar to those described in Chapters 3 and 4. Due to requests by the Yomiuriland Marine Aquarium management not to enter the water, a modified plexiglass apparatus was built.

Two PVC tubes were attached to a sheet of plexiglass with holes drilled through it at 10 cm intervals. Each of these tubes were 1.8 cm (3/4 in.) in diameter and equaled the length of the plexiglass. Three pieces of PVC tubing 1.25 cm (1/2 in.) in diameter were constructed in a "U" shape and placed in the aquarium close to and parallel to the underwater viewing window. The positioning of this piece of the apparatus was such that the bottom of the "U" rested upon the bottom of the tank and was secured there by two large suction cups while the open end of the "U" extended up one floor to an observation platform above the tank. Right and left sides of the "U" were secured to a metal railing. The width of the "U" shaped PVC tubing equaled the width of the plexiglass with the larger PVC tubing attached. The bottom of these larger tubes with the plexiglass in between were then centered over the top of the smaller tubes of the "U" shaped tubing and lowered so that the plexiglass could slide up and down the length of the "U" shaped apparatus in guillotine-like fashion. A rope attached to the plexiglass facilitated the raising and lowering of the plexiglass (Figure 28). This design enabled us to fill the plexiglass with vegetation and present it to both manatees without entering the water. The distance between the underwater viewing window and the plexiglass was < 0.5 meters. The increased distance between the videocamera and the plexiglass did not effect the quality of the videotape compared to directly attaching a plexiglass apparatus to the window. One downfall of this design was that the large Amazonian fish which were kept in the same tank with the manatees occasionally swam between the plexiglass and the underwater window, obscuring the view of the manatee feeding upon the plexiglass. Usually this was momentary and of little hindrance to collection of data. In addition, manatees were videotaped through the underwater viewing window feeding upon free floating vegetables (which



varied from day to day) to determine if differences existed between feeding upon floating vegetation versus submerged vegetation.

Only feeding trials in which sirenians ate approximately 80 to 90% of the vegetation presented were used for data analysis and calculation of mean feeding rates. Behavior of all sirenians was recorded using a Yashica model KD-H170u Hi8 format video camera and evaporated Hi8 videotape. Videotapes of dugong and manatee behavior were analyzed in real time, slow motion, and frame by frame to determine the component movements of the bristles, snout and associated structures. Analysis of videotape was performed in Gainesville, Florida on a Panasonic model AG-7300 S-VHS editor in conjunction with either an IBAS computer imaging system (Kontron Image Analysis Division) which supported a black and white imaging monitor or a Sony Trinitron model PVM-1350 color video monitor.

## Results

### External morphology

#### Dugongs

The shape of the dugong oral disk differs from that of the manatee. The basic shape of the upper lip when relaxed is a half-oval or horseshoe viewed face-on. The distance between the nares and the oral disk is greater in dugongs than manatees due to the increased angle of deflection of the rostrum. The ventral margin of the oral disk is straight and continuous from one side to the other; there are no hanging pouches or similar structures in the dugong as found in the manatee (see Figure 2C, Chapter 2 and Figure 34, Chapter 7). Five creases mark the oral disk: a single shallow crease down the midline, and a pair

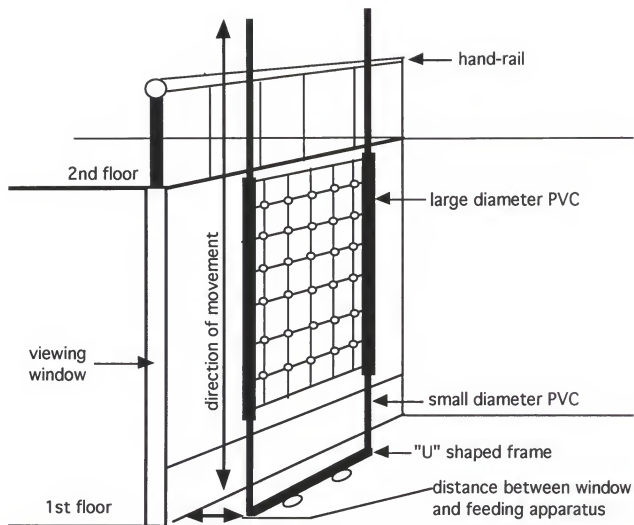


Figure 28. Schematic showing modified version of a Florida manatee plexiglass feeder. The plexiglass slides up and down on "U" a frame constructed of PVC. Not drawn to scale.

of deeper creases at each lateral edge. Such creases are not found in manatees. The paired lateral creases mark a fold of skin which is tucked away from view when the animal is not exploring its environment or feeding. During feeding or exploring, the muscles in the local region of the lateral creases appear to relax and the lateral pair of creases disappears. This extends a large portion of skin or marginal flaps from each lateral edge of the oral disk. The addition of these flaps coincides with a change in shape of the oral disk from relatively

narrow and rounded to wide and flattened. These lateral flaps increase the surface area of the oral disk and give it a more circular appearance. This phenomenon is documented in photographs (in Reynolds and Odell, 1991, page 156) although no mention is made regarding this structure. The behavioral protrusion of this anatomical structure is very similar to the "flare" behavior in the manatee (Chapter 3). Along the entire caudal edge of the oral disk of the dugong (medial to lateral) are modified vibrissae similar to those found in manatees. These bristles appear longer and more slender than manatee bristles (personal observation). Dugong bristles along the midline of the ventral edge of the oral disk appear fewer in number and shorter than those found at the lateral margins. Dugong bristles found at the ventral lateral margin of the oral disk are organized in a group very similar to the U2 group of bristles found in the upper manatee lip. In fact, the two regions appear to be similar and homologous. This becomes even more apparent when viewing the use of these regions during feeding behavior.

#### Amazonian and Antillean manatees

The shape of the upper lip in the Amazonian and Antillean manatees is a complete oval. When relaxed, the lateral-ventral portions of the oral disk hang below the remainder of the oral disk as suspended pouches. This shape is similar to that of Florida manatees. (see Figure 2C, Chapter 2 and Figure 34, Chapter 7). These "pouches" in larger Florida manatees appear accentuated (personal observation). Within these pouches are short stiff modified vibrissae often referred to as bristles (Hartman, 1979). These bristles in Amazonian and Antillean manatees are used in combination with similar bristles on the lower jaw to facilitate feeding. When the Amazonian and Antillean manatees were

investigating food or unfamiliar objects in their environment, the perioral region was "flared" or increased in surface area, which also exposes the bristles on the upper lip (again, similar to Florida manatees, Chapter 3). The Amazonian and Antillean manatees appear to possess bristle fields identical to those found in Florida manatees. During this phase of investigation, both Amazonian and Antillean manatees touched food and objects with bristle-like hairs (which cover the oral disk) in a similar manner to that described for Florida manatees (Chapter 3). This behavior is likely the result of contraction of the muscles of facial expression as found in Florida manatees (Chapter 4), and it usually occurs when tactile investigation or ingestion commences.

#### Behavioral Use of Perioral Bristles

#### Dugongs

During the first two days of data collection, the female dugong, Serena, had some difficulty positioning herself upon the plexiglass. However by day three of data collection, she immediately swam to the plexiglass, positioned herself correctly and began to feed. Feeding trials with the male dugong proved more difficult. The male, Jun-Ichi, was timid and not as docile as the female dugong. I was told by a dugong keeper that this was because he was captured as an older animal and not hand-raised as was the female dugong. Attempts to record feeding behavior were conducted following feeding trials with Serena. Jun-Ichi would timidly approach the apparatus often and consistently. However he would only feed for 20 to 30 seconds and then swim away.

The use of the perioral bristles during feeding behavior in dugongs is quite different despite the apparent homologous nature of the structures in dugongs and manatees. Like manatees, dugongs also use the perioral bristles in a cyclic prehensile fashion (Figure 29). However, in dugongs the pattern of movement is opposite to that found in manatees. The cycle is as follows:

- A. The pair of lateral creases relax and the extra flap of skin is extended in a flare-type behavior
- B. Movement begins at the midline; the upper lip is lifted slightly to either side of the central crease of the oral disk simultaneously; the margin of the lip at this lifted point curls rostrally in a behavior which I call a "pucker"; when this behavior occurs, the upper lip forms a small "M" shape.
- C. This lifted and puckered portion then travels laterally in a wave action, the puckering action functioning to protrude the perioral bristles. At this time the lower jaw begins to open.
- D. At the lateral-ventral margin of the oral disk, this wave runs into the homologue of the U2 bristle field in manatees. The lower jaw is completely open.
- E. This large group of bristles sweeps forward (rostrally), then laterally, and then caudally, sweeping any vegetation caught lateral to the mouth inside the oral cavity. The L1 bristles on the complete opened lower jaw protrude and the lower jaw begins to close; vegetation is pushed into the oral cavity.

The movements of jaw closure and bristle protrusion appear to be same as in manatees, even though bristle movement is reversed. Observations of dugongs feeding from a distance reveals that the rostral region is continually thrust forward and backward. This action pushes seagrass to the side and facilitates grasping of the vegetation by perioral bristles on the lateral-ventral region of the upper oral disk (Figure 29). Dugongs fed exclusively upon a single vegetation, the temperate seagrass *Zostera marina*. The mean feeding cycle length for Serena is 791 ms (S.D.  $\pm$  41.6)(Figure 30) and ranged from 738 ms to 899 ms.

Figure 29. Sequence of movements of perioral bristles, lips and jaw of dugongs during feeding on *Zostera marina*. A-E refer to component movements listed in text.



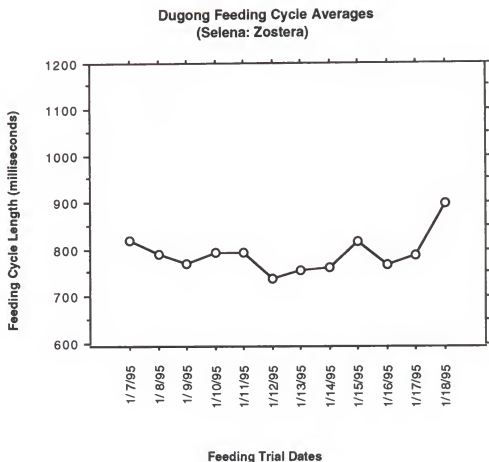


Figure 30. Feeding trial data from one captive dugong (female). Each data point represents the mean for each trial day. Mean feeding cycle length = 791.4 ms (S.D.  $\pm$  41.6)

#### Amazonian and Antillean manatees

As in Florida manatees (Chapter 3), feeding principally involved the engagement of the large and robust perioral bristles fields of the upper lip in a prehensile, grasping manner. The sequence of observed movements is as follows:

- A. The most rostral muscular portion of the snout contracts in the rostro caudal direction. This action pulls the oral disk dorsally and exposes the U2 bristles to the vegetation.



- B. The U2 bristles evert forward then are moved medially to bring the plant material toward the midline of the body in a lateral to medial sweeping motion. The lower jaw begins to open at this time.
- C. The right and left U2 bristles reach apposition at the midline and push vegetation into the oral cavity; the lower jaw is now maximally open. The L1 bristles evert from their fleshy pad.
- D. The U2 bristles diverge laterally and the lower jaw begins to close.
- E. As the lower jaw closes, the L1 bristles sweep vegetation further caudally into the mouth. The U2 bristles arrive at their original and lateral position. A new grasping cycle then begins.

The Amazonian manatee fed upon parsley (*Petroselinium crispum*), *Hydrilla*, *Myriophyllum* and *Vallisneria*. Mean feeding cycle length when feeding upon parsley was 802 ms (S.D.  $\pm$  19.0) (Figure 31) and ranged from 779 ms to 823 ms. The feeding cycle lengths of the Amazon manatee feeding upon *Hydrilla*, *Myriophyllum* and *Vallisneria* were 770 ms, 779 ms, and 782 ms, respectively. The mean feeding cycle length for these natural plants was 777 ms (S.D.  $\pm$  6.3)(Figure 32).

## Discussion

### Morphology

Despite the marked differences in snout morphology of dugongids and trichechids, the underlying musculature is surprisingly similar (Domning, 1977, 1978; Saban, 1975; Gambaran and Sokolov, 1986; Chapter 4). Muscles employed in the use of perioral bristles during feeding in Florida manatees are all muscles of facial expression in other taxa (i.e., *orbicularis oris*, *levator nasolabialis*, *lateralis*

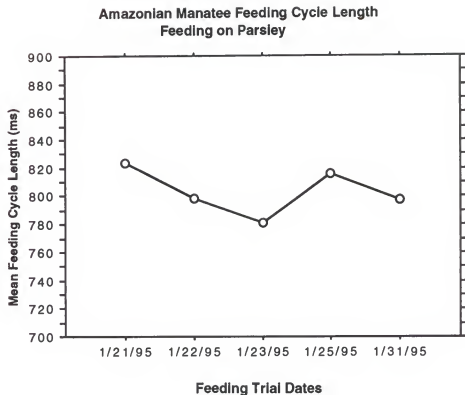


Figure 31. Feeding trial data from one captive Amazonian manatee (female). Each data point represents the mean of a single feeding trial. Mean feeding cycle length = 802 ms (S.D.  $\pm$  19.0).

*nasi*, *sphincter colli profundus pars oris*, *mentalis*, *buccinator* and *maxillonasolabialis*). Due to differences in degree of rostral deflection within Sirenia, slight variation of insertion and origins of muscles exist, but overall the relative positions of the muscles are similar.

The Amazonian and Antillean manatee feeding apparatus allows for flexible manipulation of food or objects in the environment. This type of apparatus is desirable for a mammal that is a feeding generalist and must be able to manipulate many different types of food with varying morphology. The dugong, however, is a seagrass specialist. It would appear that the most efficient way to harvest small delicate seagrasses that are highly digestible (Preen, 1992) is to possess a feeding apparatus which creates a wedge (rostral

portion of the oral disk) that lays seagrass on the side as the animal moves over the seagrass bed. This behavior increases the number of plants that can be grasped at one time (by laterally moving perioral bristles).

Anderson (1979) provided a good description of the oral disk and the perioral bristles. He reported that the oral disk ". . . represents a greatly expanded upper lip, separated from the mouth posteriorly by a bulbous connective tissue pad of uncertain origin." Domning (1977) reported that the snout and disk musculature are extremely complex. The lateral and posterior margins can be separately and precisely controlled and when used in

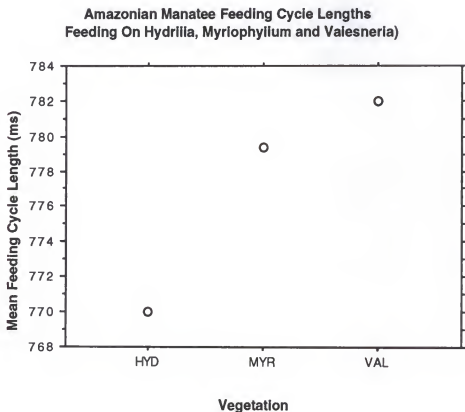


Figure 32. Feeding trial data from one captive Amazonian manatee (female). Each data point is the mean for a single feeding trial. Mean feeding cycle length = 777.11 ms (S.D.  $\pm$  6.3). HYD = *Hydrilla*, MYR = *Myriophyllum* and VAL = *Vallisneria*.

coordination with the enlarged poster-lateral bristles, function like opposable digits or forceps to grasp plant material and convey it to the mouth.

### Feeding Behavior

The mean feeding cycle length of the female dugong (791 ms) was longer than that for Florida manatees (610 ms). Several reasons which may possibly explain this difference are: (1) the dugong feeding cycle is more complex than that of manatees, correlated with a specialized feeding niche compared to a generalist feeding niche; (2) the large differences in morphology and function of the dugong upper and lower cornified horny pad of the rostrum and teeth; (3) dugongs fed upon a single species of vegetation compared to five species fed to Florida manatees or (4) there is an effect of body length on the mean feeding cycle in dugongs. Data from Florida manatees suggests that vegetation morphology may effect feeding cycle rates (Chapter 5). *Zostera* is a seagrass with single long, wide blades. It is similar in size and shape to *Vallisneria* (a freshwater species) and similar in shape to the seagrass *Thalassia*. (*Thalassia* is shorter and not as wide) However, mean feeding cycle lengths of Florida manatees feeding on *Vallisneria* and *Thalassia* (613 ms and 641 ms, respectively) are still well below the mean feeding cycle length for the dugong (791 ms). The body length of sirenians in this study is summarized in Table 8. Body length of Florida manatees in the previous was significantly longer (281 cm). Shorter Florida manatees appear to have shorter mean feeding cycle lengths (see Figure 25 and 26, Chapter 5). Based on the regression relationship of Florida manatee mean body length to mean feeding cycle length, it would be expected that the mean dugong feeding cycle length would be shorter than measured. The dugong mean feeding cycle length is 35% longer than estimated (584 ms) based

Table 8: Body length of individual sirenians

<u>Individual</u>	<u>Species</u>	<u>Length</u> (cm)
Jun-Ichi	<i>Dugong dugon</i>	252
Serena	<i>D. dugon</i>	256
Mammi	<i>Trichechus inunguis</i>	260*
Antillean	<i>T. manatus manatus</i>	220*

\*Visually estimated by animal care taker (Mr. Masumitsu Iwata)

the regression relationship between body length and feeding cycle length for Florida manatees (Chapter 5). It is questionable whether such a regression analysis for Florida manatees can be applied to dugongs. The data support the hypothesis that dugong body length may scale with feeding cycle length differently, and perhaps in a different direction, compared to Florida manatees. However, when mean feeding cycle length is converted to a rate (its inverse), the dugong feeding rate (1.26 "chews" per second) is within values reported for manatees in this study.

During the first days of the feeding trial the Amazonian manatee was very reluctant to eat from the plexiglass. In order to persuade the animal to feed from the apparatus, parsley, which is a favorite item for this individual, was presented on the plexiglass. The mean feeding cycle length of the Amazonian manatee feeding on parsley was 802 ms. The morphology of parsley is different than that of any vegetation presented to Florida manatees. Parsley is also a terrestrial plant and therefore has a higher fiber content than aquatic vegetation. Therefore, any comparisons between the Amazonian manatee feeding on parsley and Florida manatees feeding on aquatic vegetation should be viewed with caution. During the last day of data collection, this individual finally fed upon the same species of plants as those presented to Florida manatees. Although each data point is a mean of one feeding trial, it is

interesting to note that the pattern of feeding cycle lengths is the same as for Florida manatees. Feeding cycle lengths for *Hydrilla* were shortest, followed by *Myriophyllum* and then *Vallisneria*. Feeding cycle lengths for each vegetation were greater in the Amazonian manatee compared to Florida manatees (Table 9).

Table 9: Mean Feeding Cycle lengths of *T. m. latirostris* and *T. inunguis* Feeding upon *Hydrilla*, *Myriophyllum* and *Vallisneria*

VEGETATION	<i>T. m. latirostris</i>	<i>T. inunguis</i>
<i>Hydrilla</i>	590 ms	770 ms
<i>Myriophyllum</i>	594 ms	779
<i>Vallisneria</i>	613 ms	782 ms

This difference is possibly related to the small sample size (subjects (N=1; feeding trials per plant species (N=1)) for the Amazonian manatee. Length of individuals may also have effected the results because feeding cycle length scales with body size (Chapter 5; Etheridge *et al.*, 1985). Although Amazonian manatees are generally smaller than Florida manatees in the wild, this may not necessarily be true for captive animals. Etheridge *et al.* (1985) found that chew rates of Florida manatees feeding upon the same species of plant varied depending upon body length; larger animals had a lower chew rate compared to shorter animals. Unfortunately, the Amazonian manatee in this study has not been measured for several years and its length could only be visually estimated (approximately 2.6 meters).

Manatees and dugongs are often considered together. However, we must remember that these species are separate at the familial level. Regarding trichechids as similar to dugongids is similar to saying that canids are similar to felids. Although many similarities exist, manatees and dugongs also exhibit divergent anatomy and behavior. Evolution has given us an interesting natural experiment. Florida manatees and dugongs are both herbivorous marine

mammals which possess similar facial musculature and modified perioral bristles (even though tooth morphology differs). Perioral bristles of the two species appear homologous. Both species are benthic in their preferred feeding habits (Hartman, 1979; Domning, 1977). However, each uses their complement of perioral bristles differently. It appears that the behavioral use of vibrissae is divergent. Such phenomena raise several unanswered questions such as: when and why did these behaviors diverge? Did ancestral sirenians possess modified vibrissae and if so how were they used? Several fossil dugongids do not show the degree of rostral deflection present in *Dugong dugon* (Romer, 1966). Sirenians were much more diverse during the Miocene. It is likely that this group possessed a rich diversity of morphology and behavior regarding use of perioral bristles for feeding.

## CHAPTER 7 OVERALL DISCUSSION AND CONCLUSIONS

### Phylogenetic Relationships

"All forms of life are, in a way, phylogenetic attainments whose special objects would have to remain completely obscure without the knowledge of their phylogenetic development (Lorenz, 1941)." "Every time a biologist seeks to know why an organism looks and acts as it does, he must resort to the comparative method (Lorenz, 1958)." In light of Lorenz's statements it is necessary to compare the structure and use of the sirenian feeding apparatus with close relatives of sirenians. However it is important to keep in mind the distance of relatedness when doing so.

The classification of the Superorder Paenungulata (Simpson, 1945) or Subungulata (Romer, 1966) has received much re-consideration recently (Inuzuka *et al.*, 1995). Included in the extant Paenungulata are the Orders Sirenia (manatees and dugongs), Proboscidea (elephants) and Hyracoidea (hyraxes). Although these groups of animals appear dissimilar, elephants and hyraxes are in fact, the closest living relatives to sirenians. All three orders possess similar morphological and molecular characteristics which set them apart from other taxa. Examples of morphological characteristics include: specialized structures for hindgut fermentation within the gastrointestinal tract, axillary mammae, development of upper incisors as tusks (dugongs but not manatees) and specialized dentition (manatees but not dugongs)(Maloiy and



Eley, 1992). Molecular investigations including amino acid sequences, hemoglobin sequences and sequences of lens alpha-crystalline protein aggregates point to a relationship among sirenians, proboscideans and hyracoideans which has led some systematists to group all three Orders in a monophyletic clade, the Superorder Paenungulata (de Jong *et al.*, 1981; Kleinschmidt and Braunitzer, 1983; Kleinschmidt *et al.*, 1986; Kleinschmidt *et al.*, 1988). In addition, of 103 vertebrate species, the evidence suggests that the Paenungulata is one of the most ancient branches of Eutheria (Maloiy and Eley, 1992). However, the number of vertebrate species examined in this analysis is small compared to the total number of extant vertebrate species.

An obvious similarity between sirenians and elephants is the elaboration of facial muscles into a muscular hydrostat (Chapter 4, Kier and Smith, 1985; Smith and Kier, 1989; Marshall *et al.*, 1996). The classic works of Boas and Paulli (1906, 1925) describe in detail the complex organization and elaboration of elephant facial muscles into a trunk. Many of these facial muscles are homologous with muscles which comprise the vibrissal-muscular complex in the Florida manatee (e.g., *M. maxillasolabialis*).

Recent anatomical investigations document the existence of vibrissae the tips of the trunks of Asian elephants (*Elephas maximus*) (Rasmussen and Munger, 1996). These vibrissae can be categorized into two groups: conventional long vibrissal hairs and vellum vibrissae (Figure 33). Vellum vibrissae are hairs which barely protrude above the surface of the skin and similar vibrissae are also found in primates (Munger, 1982). The two types of vibrissae reported in the Asian elephant lack the conus innervation that is a prominent feature of vibrissae used for whisking behavior (Rice *et al.*, 1986). In addition, there are no cutaneous muscles surrounding elephant vibrissae, which supports the contention that vibrissae in Asian elephants are not mobile.

The similarities between sirenian vibrissae and elephant vibrissae are limited to the rostral location where vibrissae are found. Although Florida manatees possess two types of vibrissae (Chapter 2), they do not possess vellum vibrissae. Although the large perioral bristles of Florida manatees (U2 and L1 fields) do lie just below the epidermis when relaxed, the degree to which they can be protruded when in use leaves no doubt that these are structures distinct from vellum vibrissae.

African elephants (*Loxodonta africana*) possess two "fingers" at the tip of the trunk and have the ability to use these structures in a prehensile fashion (Bets Rasmussen, personal communication). In contrast, Asian elephants (*Elephas maximus*) do not possess a prehensile ability using their single "finger" but can wrap their entire trunk around objects for manipulation (Sukumar, 1989). However, it appears that elephants do not use the finger apparatus in conjunction with specialized vibrissae to manipulate food and objects. Although sirenians and elephants are similar in that both possess specialized and elaborate oro-facial musculature, they are divergent with regard to use of vibrissae. In addition, specialized oro-facial anatomy is not unique to sirenians and elephants. The coati (*Nasua nasua*) possesses a mobile rostrum which is used for foraging (Compton, 1973). Thus, in sirenians, modification of vibrissae in conjunction with a specialized muscular organization (muscular hydrostat) enables use of the bristles in a prehensile manner and is a departure from the classical mammalian plan (and from elephants) for vibrissal function.

Although elephant and hyraxes are the closest living relatives to sirenians, each group is greatly diverged from each other compared to other mammalian taxa. A phylogenetic comparison in this group is rarely satisfying. Historically, sirenians have been compared with other herbivores, mostly

Figure 33. Asian elephant trunk tip. DT = dorsal tip, LVH = large vibrissal hairs, LDT = lateral dorsal tip, SVH = small vibrissal hairs, VT = ventral tip. (Rasmussen and Mungler, 1996. Reproduced with permission, Wiley and Sons, Inc..



terrestrial, except for references to green turtles (Bjorndal, 1979; Lanyon *et al.*, 1989, Lanyon, 1991; Preen, 1992). The comparison to terrestrial herbivores is of obvious significance due to similarities in feeding niches and similar comparisons will be made below. However, life in an aquatic environment imposes certain constraints which cannot be ignored, and comparisons with other marine mammals may also be illuminating.

### Vertebrate Feeding Musculature

Comparison of the feeding apparatus of sirenians with those of terrestrial vertebrates is difficult. This is due to the fact that most investigations of the feeding mechanics of vertebrates (including terrestrial herbivores) examined have focused on intra-oral events, especially on mastication and the mechanics of jaw muscles and skeletal components (for example, Hiimae, 1978; Franks *et al.*, 1985; Hiimae and Crompton, 1985; Busbey, 1989; German and Franks, 1991; Reilly and Lauder, 1991; Anderson *et al.*, 1992; Cleuren and De Vree, 1992; Dessem and Druzinsky, 1992; Reilly and Lauder, 1992; Weishampel, 1993; Elwood and Cundall, 1994; Motta and Wilga, 1995). Relatively little research has been conducted on soft tissue structures such as the sirenian feeding apparatus. Invertebrate soft tissue anatomy has received much attention (see Chapman, 1958, 1975 for reviews). Muscular hydrostats have been studied extensively, mostly in invertebrates, and especially in molluscs (Kier, 1982; Kier and Smith, 1985; Kier, 1989). Only recently have muscular hydrostats in vertebrates received much attention and this has been concentrated on the form and function of tongues (Lowe, 1981; Smith, 1984, 1986, 1988; Wainwright and Bennett, 1992a, 1992b). However, muscular

hydrostats are not limited to tongues but also include lips and proboscises (Wainwright, 1988).

The facial myology of many vertebrates has been described (e.g., Boas and Paulli, 1906, 1925; Huber, 1930a, 1930b; Lightoller, 1928, 1934, 1940a, 1940b, 1942; Minkoff *et al.*, 1979) especially that of domestic animals (see Getty, 1975; Sisson, 1975a, 1975b; St. Claire, 1975), and in particular the domestic dog (Evans and Christensen, 1979), but few have examined such structures from a functional perspective. As addressed in many of these papers, the question of homology and evolution of facial muscles is still of interest today, particularly from a functional standpoint. For example, Huber's (1930a, 1930b) suspicion that the *M. maxillonasolabialis* was really a derivation of the *M. buccinatorius* was confirmed using phylogenetic, comparative methods (Minkoff *et al.*, 1979). The unusual extension of the *M. buccinatorius* and increase in size of *M. maxillonasolabialis* in manatees can be viewed as the result of a progression toward increasing complexity in oro-facial anatomy. It is plausible that selection pressure for increased feeding efficiency in aquatic herbivores has resulted not only in (1) a spectrum of rostrum deflection in all sirenians, and (2) supernumerary and rootless cheek-teeth in trichechids and dugongids, respectively, but also, (3) in the form and function of the sirenian oro-facial anatomy (including perioral bristles) present today. It is likely that early sirenian ancestors possessed a simple facial myology relative to extant species. Natural selection for aquatic herbivory might have involved such derivations of new muscles from pre-existing muscles. Such derivations could in turn have resulted in new functional capabilities. Additional functional derivations and increasing complexity may have eventually led to a facial musculature which is organized as a muscular hydrostat. By analogy, it is well known that current

tooth morphology and rostrum deflection in both trichechids and dugongids are evolutionary derivations from ancestral conditions (Domning, 1982).

Although functional questions regarding the anatomy of the orofacial region in terrestrial herbivores have not been answered in detail, some ecological correlations have been observed. A functional relationship between foraging ecology and morphology of the feeding apparatus is apparent among terrestrial herbivores. Although sirenians are unique in the manner which they attain a prehensile ability, prehensile-ness is a common phenomenon among herbivores. Whereas sirenians use modified vibrissae and facial musculature to grasp food, terrestrial herbivores exhibit a diversity of solutions to achieve prehensile functions. For example, the giraffe (*Giraffe sp.*) uses its tongue and prehensile lips to grasp and browse foliage (Dagg and Foster, 1976). The tongue can grow as long as 54 cm and 8 cm wide (Schneider, 1951). During feeding the tongue is wrapped around groups of leaves or fruit to pull them to the lips, where the food is manipulated further, or into the mouth directly (Dagg and Foster, 1976). The giraffe tongue possesses greater mechanical power than that of any other ungulate (Sonata, 1922). The okapi (*Okapi johnstoni*), another giraffid, also possess a manipulative tongue which can be up to 30 cm long and 4.5 cm wide (Burne, 1917).

Tapirs (*Tapirus sp.*) possess a long proboscis which is prehensile in nature and is used in foraging to pull leaves and fruits from plants and to manipulate fallen fruit (Terwilliger, 1978). In general, it appears that all tapirs are browsers (Medway, 1969, 1974; Terwilliger, 1978). Although the proboscis is important in many aspects of daily life and social behavior of tapirs, little data are available on this structure.

Species of rhinoceroses exhibit differences in lip morphology which are correlated with browsing versus grazing feeding behavior. These features are

exemplified in the resource partitioning of African rhinoceroses. Black rhinoceroses (*Diceros bicornis*) possess a narrow, beak like upper lip structure and are considered adapted for browsing (Goddard, 1968; Shenkel and Lang, 1969; Owen-Smith, 1975; Eisenberg, 1981). White rhinoceroses (*Ceratotherium simum*) possess broad, wide lips and are considered to be adapted to grazing (Shenkel and Lang, 1969; Eisenberg, 1981). Such divergence in lip morphology and foraging ecology is analogous to the foraging strategies of manatees and dugongs. The feeding apparatuses of manatees and dugongs are divergent, Manatees appear to possess high tactile discrimination ability (personal observation) despite their generalistic feeding habits; many plants are consumed by cropping off the top half (Hartman, 1979) much like a browser. This behavior is reflecting in the form of the feeding apparatus, which is narrower than dugongs, and the movement of bristle fields to the midline in order to pinch off portions of plants. Dugongs, although also prehensile, do not appear to have as high a degree of tactile discriminatory abilities as do manatees (personal observation); their rostrum is much wider than manatees and bristles are moved in a medial to lateral direction. Dugongs are adapted to bottom-feeding and their foraging ecology is more reflective of a grazer, although browsing does occur (Preen, 1992).

#### Comparisons with Green Turtles

The green sea turtle (*Chelonia mydas*) is the only reptilian species to feed extensively upon seagrasses and/or algae (Mortimer, 1976; Bjorndal, 1979, 1980, 1985). They feed exclusively on algae or seagrasses but not a mixture of the two. Individuals may possess different gut flora required for the breakdown of seagrasses versus algae (Bjorndal, 1979; 1985). Turtles which normally feed



upon seagrasses but were force fed algae in captivity exhibited low digestibility efficiency which was reflected by large pieces of undigested algae present in feces (Bjorndal, 1980, 1985). Changes in digestibility have also been implicated for sirenians as well; sirenians may refrain from feeding upon algae because their gut flora has difficulty digesting it (Bjorndal, 1979, 1980, 1985). In order to increase digestion efficiency, green turtles return to selected areas of seagrass to crop and re-crop blades. Such re-cropping maintains new growth of seagrasses which are low in lignin and therefore more digestible (Bjorndal, 1979, 1980, 1985; Thayer *et al.*, 1984). Dugongs in sub-tropical regions have been reported to return to selected meadows of seagrasses to re-crop new growth. This has also been interpreted as "cultivating" new growth of seagrass in an effort to increase its nutritional value (Thayer *et al.*, 1984; Preen, 1992). This type of foraging behavior has been suspected but not reported for manatees (Lefebvre and Powell, 1990). In the upper Banana river (Cape Canaveral, FL) groups of manatees are observed to return to selected areas to feed upon seagrasses, ignoring adjacent areas of seagrasses which appear equal in quality (Jane Provancha, personal communication).

#### Vibrissae Elaboration in Mammals

The classical function of mammalian vibrissae is to obtain tactile information from the environment (Ling, 1977). Tactile cues are important to all mammals. However, certain mammals have elaborated upon vibrissal form, density and even function. Pinnipeds are a group known for their well developed vibrissae (Hyvärinen, 1984, 1989; Fay, 1982; Ling, 1966, 1977). Most notably, the walrus and bearded seal have very dense arrays of elongated vibrissae (Fay, 1982; Kastelein and van Gaalen, 1988, Kastelein *et al.*, 1990;

Reidman, 1990). Since sirenians also exhibit specialized vibrissae, it is useful to ask how the form and function of marine mammal vibrissae compare with those of terrestrial taxa. Vibrissae relay vibrotactile information concerning static displacement of sinus hair follicles to the central nervous system, in some cases incorporating a degree of directional selectivity (Burgess and Perl, 1973; Dykes, 1975; Gottschaldt *et al.*, 1973). Displacement of the hair follicle stimulates mechanoreceptors (e.g., Merkel cells) in a glassy sheath membrane surrounding the outer root of a single vibrissa. The number of Merkel cells in a single vibrissa of a Lake Saimaa ringed seal (*Phoca hispida saimensis*) ranges from approximately 10,000 to 20,000; the number of lanceolate endings ranges from 1,000 to 4,000 (Hyvärinen, 1995). In comparison, Merkel and lanceolate receptors of terrestrial mammals range from 500 to 2,000 and 20 to 100, respectively (Halata, 1993; Hyvärinen, 1995). This large difference in receptor numbers suggests that ringed seals (and possibly other marine mammals) rely heavily upon tactile senses and possess higher tactile discriminative ability compared to terrestrial taxa. Harbor seals (*Phoca vitulina*) can discriminate objects using their vibrissae as effectively as monkeys can discriminate using their hands (Denhardt and Kaminski, 1995). Significant differences in vibrissal structure also exist between terrestrial and aquatic taxa. Vibrissae of southern elephant seals, (*Mirounga leonina*) and ringed seals consist of a large blood sinus in a collagenous capsule that surrounds the hair follicle and is divided into three regions: a lower cavernous sinus, a central ring sinus and an upper sinus, each compartmentalized by connective tissue (Hyvärinen, 1984, 1989; Ling, 1966, 1977). The ringwulst, a collar-like projection surrounding the lower part of the central ring sinus, may control blood flow and pressure inside the capsule and thereby affect sensitivity thresholds of its mystacial vibrissa (Ling, 1966, 1977). Only an upper and lower ring sinus have been documented in

terrestrial mammals (Davidson and Hardy, 1952; Melaragno and Montagna, 1953) and some lack a ringwulst (Hollis and Lyne, 1974; Marotte *et al.*, 1992).

In contrast, vibrissae in cetaceans are small, reduced or absent (Yablokov and Klevezal, 1964; Ling, 1977). However, during development and soon after birth, many odontocetes possess vibrissae. As these whales become older the vibrissae fall out and become vestigial follicles or "pits." This suggests that vibrissae may also have been important to cetaceans at one time in their evolutionary history. Indeed, vibrissae are still present in many mysticete species and in some species of odontocetes (e.g., *Plantanistidae*). Vibrissae in plantanistids are well developed throughout life in the form of bristles on the upper and lower jaw of the slender snout (Norman and Fraser, 1948; Ling, 1977). It is reasonable that the evolution of echolocation in odontocetes may have displaced much of the need for vibrissae, whereas mysticetes, which possess only a limited ability to echolocation still possess functional (albeit limited) vibrissae.

I have shown that large differences in vibrissae form and function exist between terrestrial and aquatic taxa. The evidence suggests that natural selection may have been strong for specialization of vibrissae in aquatic mammals. It is possible that mammals living in the aquatic environment have a greater need for a higher resolution of tactile information compared to terrestrial taxa. Many species dive to great depths to feed, where vision is temporarily no longer useful (e.g. elephant seals and sperm whales) or spend large amounts of time in water of limited visibility (e.g., river dolphins)(Ling, 1977; Scheffer, 1976; Reidman, 1990; LeBoeuf *et al.*, 1993). If vibrissae are used in connection with prey capture by marine mammals then the increased ability to discriminate may indicate that either (1) aquatic prey are more elusive than terrestrial prey, or (2) discrimination of non-elusive prey (or plants) may be of

greater importance or of greater ease in the aquatic environment. This may be especially true of those marine mammals that are benthic in their feeding habits.

#### Comparisons of Vibrissae of Several Benthic Feeding Marine Mammals

The structure of Florida manatee vibrissae (bristles) differs from that of any other taxa for which data are available. Their vibrissae are short, thick, and smooth and are surrounded by complex facial musculature; smaller and thinner sinus hairs cover the rest of the snout (Chapter 2). The microanatomy of manatee bristles appears poorly developed; only the ring sinus is well developed and a ringwulst is absent (Dosch, 1915). Sirenians use these short, stout bristles and the surrounding facial muscles in a prehensile manner to bring vegetation manually into the oral cavity. The primary function of the sirenian vibrissae is to grasp vegetation; sensory function is likely secondary and probably fulfilled by the numerous short sinus hairs that cover the most rostral portion of the snout (Chapter 2).

Walrus possess a large number of smooth vibrissae (600-700)(Reidman, 1990) on the anterior region of their broad and flat muzzle. Little is known of walrus vibrissae ultrastructure. The capsule of the vibrissae is surrounded by blood sinuses typical of a sinus hair and a ringwulst is present and larger than reported for *Mirounga* (Ling, 1966; Fay, 1982). Wear pattern of vibrissae and behavioral observations of captive animals suggest that vibrissae are used for foraging in the substrate. Captive walrus that cannot feed naturally have longer vibrissae than wild walrus. It appears that mystacial vibrissae are used to detect and discriminate prey items (Fay, 1982). Walrus vibrissae share the combination of manipulative and sensory functions with sirenians (Fay,

1982; Kastelein and van Gaalen, 1988; Kastelein, *et al.*, 1990). For example, captive walruses can move small pieces of clams toward the mouth with individual vibrissa (manipulative ability) (personal observation). However, my findings indicate that walruses can not grasp objects (prehensile ability). Even so, anecdotes exist which suggest that walruses can use vibrissae in a prehensile manner. For example, an individual at the Brookfield Zoo was observed picking up a basketball with its vibrissae (James Mead, personal communication). However, it is more likely that the basketball was picked up using its suction ability. These animals rely more upon their suction ability than upon vibrissae to introduce food into the oral cavity, and the pressures created can be quite large (Kastelein *et al.*, 1994, 1996).

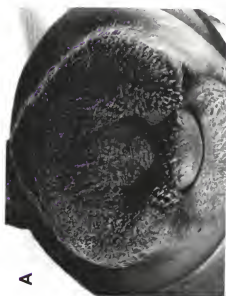
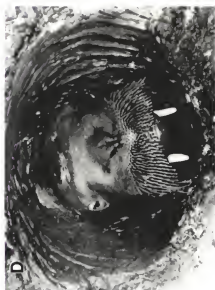
Bearded seals possess very prominent vibrissae, as their common name suggests. Vibrissal shafts of bearded seals have a smooth appearance when cut longitudinally; the width of the shaft is constant. Vibrissal shafts in other phocids are beaded and exhibit a wave appearance when cut longitudinally; *Erignathus* and *Monachus* species (Monk seals) are the only phocids to possess smooth vibrissae, a characteristic that they share with all otariids, walruses and sirenians (Denhardt and Kaminski, 1995). The vibrissae of *Erignathus* often curl when dry, indicating that they may not be as rigid as walrus vibrissae. Bearded seal vibrissae may function to help discriminate prey animals (King, 1964; Nowak and Paradiso, 1983); this assumption seems reasonable due to the dietary overlap with walruses, which have high discriminatory abilities (Kastelein and van Gaalen, 1988; Kastelein *et al.*, 1990). Bearded seal vibrissae may also function in a coordinated manner (e.g., walruses and sirenians) to manipulate the substrate, rather than in a whisking motion (e.g., most pinnipeds). However, nothing is known regarding the functional morphology of bearded seal vibrissae at this time.

### Marine Mammal Benthic Foragers

Among marine mammals, Florida manatees and dugongs share certain ecomorphological traits with walruses and bearded seals despite their different evolutionary histories (Figure 34). All are primarily or obligatory benthic foragers, and feeding occurs at relatively shallow depths. Perturbation of the substrate results from feeding and effects the benthic community upon which they feed. Walruses and sirenians exhibit a convergence of morphological and behavioral characteristics, including elaborate vibrissae, well-developed facial muscles, complex innervation for fine motor control of vibrissae, increased width of the rostrum, broad cranium, large body size and reduction in size of the eyes (Domning and Hayek, 1986; Fay, 1982; Kastelein *et al.*, 1991a, 1993; Murie, 1872, 1880; Reynolds and Odell, 1991). Walruses and sirenians use their vibrissae as exploratory and manipulative tools during feeding (Vrolik, 1852; Murie, 1872, 1880; Chapman, 1875; Garrod, 1879; Vibe, 1950; Mohr, 1957; Allsopp, 1961, 1969; Fay, 1982; Kastelein and van Gaalen, 1988; Kastelein *et al.*, 1990; Marshall and Reep, 1994; Marshall and Reep, 1995b; Marshall and Reep, 1995c; Marshall *et al.*, 1995). The functional relationship between feeding and vibrissal use is best known for sirenians (Marshall and Reep, 1994; Marshall and Reep, 1995b; Marshall and Reep, 1995c; Marshall *et al.*, 1995, this study). Although there have been anecdotal observations of vibrissae use during walrus feeding, no study has characterized the movement patterns of walrus vibrissae (Fay, 1982; Kastelein and van Gaalen, 1988; Kastelein *et al.*, 1990; Vibe, 1950). To date, there has also been no systematic study of vibrissae function in bearded seals (Ian Stirling, Kit Kovacs, personal communication).

Bearded seals (*Erignathus barbatus*), named for their large mystacial vibrissae and deep jaw, are the largest of the arctic phocids. Their distribution

Figure 34. Facial region of marine mammal benthic foragers. A. Florida manatee, B. Dugong, arrows indicate extendible margin of oral disk. C. Bearded Seal, D. Walrus. B Provided by Danni Tikel. C. taken from Reidman (1990), original photo by Kathy Frost.





is circumpolar boreoarctic and two subspecies are recognized (King, 1964). Bearded seals feed on benthic fauna in relatively shallow water, less than 130 meters deep (Burns, 1981; Chapskii, 1938). Their distribution seems to be strongly skewed toward regions of shallow water and high biomass (Kelly, 1988). Seals from the Okhotsk Sea eat a large variety of prey including 41 species of benthic and nektonic invertebrates (Fedoseev and Bukhtiyarov, 1972). A wide variety of invertebrates are eaten, but decapod crustaceans and molluscs constitute the majority of the diet throughout the bearded seal's range (Burns, 1967, 1981; Chapskii, 1938; Johnson *et al.*, 1966; Kenyon, 1962; Kosygin, 1966, 1971; Lowry *et al.*, 1977, 1978, 1980, 1982; Pikharev, 1940).

The bearded seal and Pacific walrus (*Odobenus rosmarus divergens*) are the only northern hemisphere pinnipeds that feed extensively upon benthic invertebrates (Lowry *et al.*, 1977). The range of Pacific walruses includes much of the Chukchi and Bering Sea, which overlap a large proportion of the range of bearded seals (Sease and Chapman, 1988). Walruses usually feed at depths between 10 to 50 meters; maximum diving depth of walruses is 79 to 80 meters (Fay, 1982; Vibe, 1950; Sease and Chapman, 1988). They feed on approximately sixty genera of benthic invertebrates, almost all of which reside at very shallow depths within the substrate and require little effort to extract (Fay, 1982). Walruses are selective when feeding in that they take only the mature age classes of the larger bivalves. It is thought that sorting or selection of prey is done primarily using the mystacial vibrissae (Fay, 1982). This selectivity may alter the structure of the benthic community, however, this relationship is poorly understood (Vibe, 1950; Fay and Stoker, 1982; Sease and Chapman, 1988). It is likely that walruses compete directly with bearded seals for benthic resources (Kelly, 1988). There is a large overlap in diet and range between the two taxa, but this relationship is also poorly understood (Lowry *et al.*, 1980).

Manatees, like walruses, change the benthic community on which they feed; increased biodiversity of seagrass beds is attributed to grazing by manatees (Packard, 1984; Provancha and Hall, 1991). Dugongs return to selected areas in which they maintain new growth of seagrasses, which makes them easier to digest due to lower fiber content (Preen, 1992). Characteristic feeding trails made by dugongs uprooting seagrasses (Anderson and Birtles, 1978; Anderson, 1979, 1989, 1994; Lanyon, 1991; Preen, 1992) are similar to feeding troughs made by foraging walruses (Fay, 1982; Nelson and Johnson, 1987; Reidman, 1990). Fay (1982) described the searching pattern by walruses for food as "more akin to grazing than to plowing or raking" and Kastelein *et al.* (1991b) described walrus searching behavior for food as "similar to the technique used by grazing animals."

The use of vibrissae by all mammals is diverse. It can be viewed as a spectrum involving sensory and motor components. In Table 10, representative taxa are used to illustrate this diversity.

Table 10. Spectrum of vibrissal use involving sensory and motor components

<-----Spectrum of Sensory and Motor Components----->

	<u>Sirenia</u>	<u>Walrus</u>	<u>Spotted seal</u>	<u>Mouse</u>	<u>Dog</u>
<u>Vibrissal Movement</u>	Prehensile	Manipulative	Whisking	Whisking	Fixed position
<u>Musculature</u>	Musculature Hydrostat	Muscular	Developed Facial muscles	Developed Facial muscles	Facial muscles
<u>Vibrissae Morphology</u>	Short/rigid thick	Long/rigid thick	Long/flexible thinner	Long/flexible thin	Reduced/thin
<u>Skull Morphology</u>	Short/broad	Short/broad	Long/thin	Long/thin	Long/thin

It has been demonstrated that sirenian use of vibrissae is unique and a departure from the common mammalian plan (Chapters 2 through 6). On the scale represented in Table 10, as vibrissal function diverges from a combined prehensile-manipulative plus discriminatory function (e.g., sirenians and walruses) and toward a purely discrimination function (e.g., spotted seal), there is little need for the placement of vibrissae in front of the snout. This difference in function is concomitant with an elongation of the skull (King, 1972; Kelly, 1988). Interaction with the substrate no longer needs to be maximized. Behaviorally, coordinated movement of vibrissae is replaced by whisking of whole fields of vibrissae (e.g., spotted seal) and, therefore, large facial muscles involved in a muscular hydrostat or coordinated manipulation of vibrissae are reduced. Whisking behavior is also seen in terrestrial taxa (Welker, 1964). Terrestrial taxa inhabit a less dense medium (air) and may not need long rigid vibrissae to perform similar functions (e.g., mice). In some taxa, such as carnivores, tactile senses are largely superseded by other senses such as olfaction and vision. In these taxa, vibrissae still provide valuable information but are relatively diminished in size and often are passive (dog).

I have shown that sirenians have an oro-facial anatomy which reflects their aquatic herbivorous feeding niche. The perioral bristles of Florida manatees have been characterized and their innervation has been determined. Behavioral use of perioral bristles have been systematically examined in Florida manatees and other sirenians (dugong, Amazonian and Antillean manatees). It has been shown that body length and plant morphology can effect the mean feeding cycle length and feeding rates of Florida manatees. Several hypotheses and speculations have been discussed regarding the possible evolution of the sirenian feeding apparatus such as derivations of new muscles from old and possible new functional capabilities arising from such occurrences. Natural

selection for a feeding apparatus which is efficient for harvesting vegetation underwater was apt to have been great. However, many similarities between the feeding apparatus of Florida manatees, dugongs and walrus exist.

Convergence on a particular form and behavior of distant two taxonomic groups with apparent divergent feeding niches (carnivory vs. herbivory) suggests that natural selection for marine mammal benthic foragers must have been greater still.

## GLOSSARY

behavioral ecology	The study of the behavior of an organism in its natural habitat, or the application of behavioral theories to particular activities.
benthic	The lowermost region of a freshwater or marine profile.
bilophodont	Teeth in which the cusps fuse to form two elongate ridges (lophs).
conspecifics	Other members of the same species.
dugongid	A member of the Family Dugongidae; a dugong.
ecological morphology	A subdiscipline of morphology which one principle entails using performance testing to link morphology to ecology.
ethology	The scientific study of the behavior of animals in their normal environment, including all the processes, both internal and external, by which they respond to changes in their environment.
extant	Applied to a taxon, some of whose members are living at the present time.
functional morphology	A subdiscipline of morphology; the study of the relationships between form and function or use.
hypsodont	Teeth which have high crowns; usually seen in herbivore mammals where the experience heavy wear.
maxilla	Region of the upper jaw.
mystacial vibrissae	A large set of whiskers which are located just lateral to the nares in most mammals; in sirenians these are also known as perioral bristles.
mysticetes	A suborder of cetaceans which possess baleen instead of teeth; whale-bone whales.
natant	Floating, usually referring to aquatic vegetation.

odontocetes	A suborder of cetaceans which possess teeth; toothed whales.
oral disk	The broad anterior-most region of the snout in sirenians, it is found dorsal and rostral to the oral cavity.
Recent	Referring to the Recent or Holocene epoch; the last 10,000,000 years since the close of the Pleistocene.
rootless cheek-teeth	Molars whose roots are open and therefore can continue to grow, usually to compensate for tooth erosion.
sampling quadrat	A square or rectangle of known area usually used for the study of or to measure the density or distribution of vegetation or animals.
substrate	The composition of the lowermost region of a freshwater or marine profile, for example a calcium carbonate substrate (coral reef/seagrass bed).
supernumerary teeth	A system of tooth replacement where molars erupt in the rear of the mouth and progressively move forward as they wear until they are shed from the front of the mouth at which point a new molar erupts in the rear of the mouth.
trichechid	A member of the Family Trichechidae; a manatee.

APPENDIX A  
NATURAL FOODS CONSUMED BY FLORIDA MANATEES

**SPECIES**

Algae  
Anabaena  
Cladophora  
Ectocarpus  
Enteromorpha  
Gracilaria

Naviula  
Oscillatoria  
Rhizoclinium  
Spyrogyra  
Vaucheria

**SUBMERGED**

Ceratophyllum demersum  
Myriophyllum spicatum  
Eleocharis acicularis  
Cabomba sp.  
Elodea densa  
Najas guadalupensis  
Ultricularia sp.  
Vallisneria spiralis  
Potamogeton pectinatus  
Hydrilla verticillata  
Hymenachne amplexicaulis  
Ruppia maritima

**SEAGRASSES**

Thalassia testudinum  
Halodule wrightii  
Syringodium filiforme  
Halophila balonis  
Halophila engelmannii

**EMERGENTS/TERRESTRIAL**

Alternanthera philoxeroides  
Panicum molle  
Panicum purpurascens  
Panicum hemitomon  
Rhizophora mangle  
Cocos nucifera  
Distichlis spicata  
Sambucus canadensis  
Paspalum vaginatum  
Phragmites communis  
Quercus sp.  
Scirpus californicus  
Serenia repens  
Spartina alterniflora  
Typha angustifolia  
Virginia repens  
**FLOATING**  
Eichhornia crassipes  
Pistia stratiotes  
Lemna sp.

References: Alsopp (1969), Hartman (1979), Best (1981), Ledder (1986).

APPENDIX B  
NATURAL FOODS CONSUMED BY AMAZONIAN MANATEES

<u>CLASSIFICATION</u>	<u>SPECIES</u>
Araceae	<i>Montrichardia arborescens</i> <i>Pistia stratiotes</i>
Convolvulaceae	<i>Ipomoea aquatica</i> <i>Operculina alata</i>
Fabaceae (Leguminosae)	<i>Phaseolus ovatus</i>
Lentibulariaceae	<i>Utricularia foliosa</i> <i>Utricularia minor</i>
Moraceae	<i>Cecropia</i> sp.
Nymphaeaceae	<i>Nymphaea</i> sp.
Poaceae (Gramineae)	<i>Echinochloa polystachya</i> <i>Hymenachne amplexicaulis</i> <i>Leersia hexandra</i> <i>Luzaiola spruceana</i> <i>Oryza perennis</i> <i>Panicum perpurascens</i> <i>Paspalum fasciculatum</i> <i>Paspalum repens</i>
Pontederiaceae	<i>Eichhornia azurea</i> <i>Eichhornia crassipes</i> <i>Pontederia cordata</i> <i>Reussia rotundifolia</i>
Salviniaceae	<i>Salvinia auriculata</i> <i>Salvinia minor</i> <i>Salvinia sprucei</i>

References: Verissimo (1895); Ferreira (1903); Pereira (1944); Rego (1944); Marmol (1976); Best (1981)



APPENDIX C  
NATURAL FOODS REPORTED FOR WEST AFRICAN MANATEES

Classification	Species
Araceae	<i>Pistia stratiotes</i>
Nymphaeaceae	<i>Nymphaea</i> sp.
Poaceae (Graminaea)	<i>Vossia</i> sp. <i>grass unspecified</i>
Polygonaceae	<i>Polygonium senegalense</i>
Pontederiaceae	<i>Eichhornia crassipes</i>
Potamogetonaceae	<i>Cymodocea nodosa</i>
Rhizophoraceae	<i>Rhizophora mangle</i>

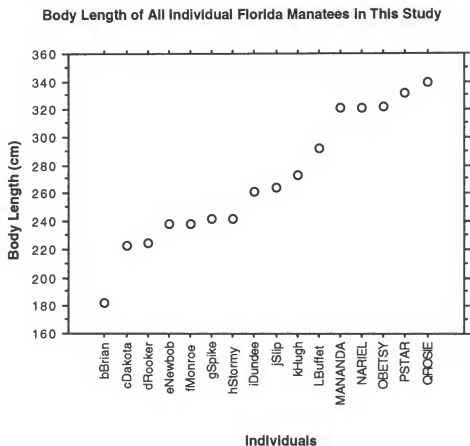
References: Perkins (1848); Shaw (1856), Beal (1939); Dekeyser (1955); Petit (1955).

APPENDIX D  
NATURAL FOODS REPORTED FOR STELLER'S SEA COW

Classification	Species
Algae	
Phaeophyta	<i>Agarum gmeline</i> <i>A. turneri</i> <i>A. pertusum</i> <i>Alaria esculenta</i> <i>Laminaria saccharina</i> <i>Nereocytis luetkeana</i> <i>Thalassiophyllum clathrus</i>
Rhodophyta	<i>Constantinea rosa-marina</i> <i>Dumontia fucicola</i>
Angiosperms	
Potamogetonaceae	<i>Phyllospadix sp.</i>

References: Steller (1899, 1925); Domning (1976).

APPENDIX E  
BODY LENGTH OF INDIVIDUALS USED IN THE STUDY



Body length data for all individual manatees in the study. Note that the first letter of each name dictates order of sequence from shortest to longest. Females names are all capitalized.

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## BIOGRAPHICAL SKETCH


Christopher Douglas Marshall was born on January 11, 1968, in Baltimore, Maryland. He graduated from Lansdowne Sr. High school outside Baltimore in May, 1986. He received his Bachelor of Science degree in biology from Virginia Tech in May, 1990 and his Master of Science degree in marine biology from Nova Southeastern University. Chris entered the Ph.D. program in the fall of 1992 and completed his requirements for the Doctor of Philosophy in the College of Veterinary Medicine in May, 1997.




I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
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Associate Professor of  
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

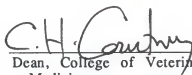
  
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